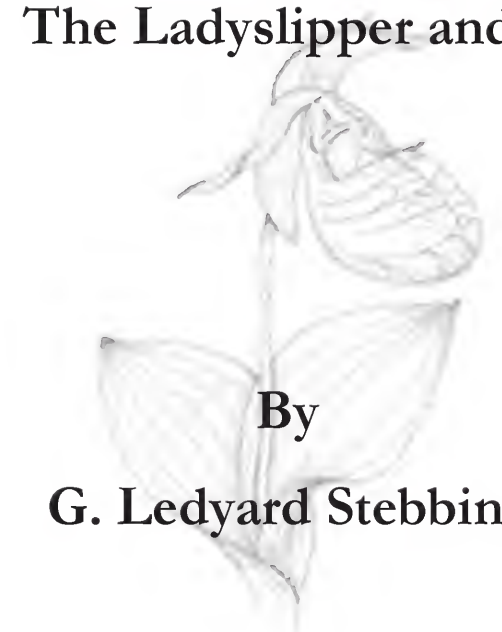
The Ladyslipper and I



By

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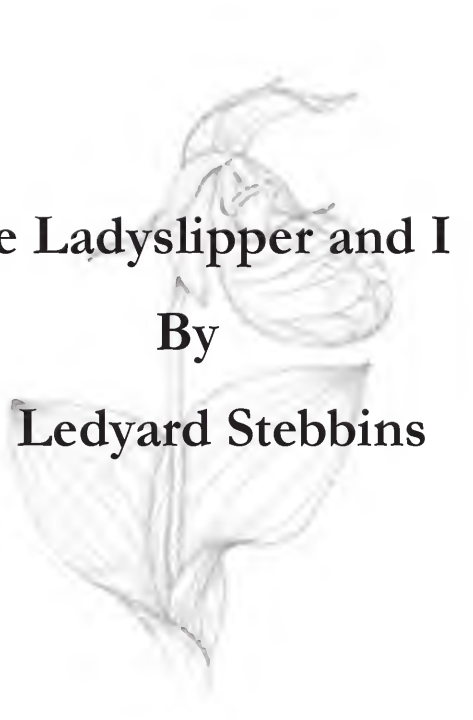
Missouri Botanical Garden



The Ladyslipper and I

By

G. Ledyard Stebbins

CALIFORNIA NATIVE PLANT SOCIETY

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Dustjacket Photograph:

G. Ledyard Stebbins Jr. leads a field trip through Carson Pass, Calfornia, circa 1967, as president of the California Native Plant Society.
Courtesy of the California Native Plant Society and GLS's personal collection

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Foreword

The Ladyslipper and I is a previously unpublished autobiographical manuscript left behind by George Ledyard Stebbins at the time of his death in 2000. A botanist in his formal training, Ledyard Stebbins's career began in 1929 while he was still a student at Harvard University, with his first publication on the flora of Mount Desert Island, Maine, an area he had explored as a child. His career rapidly grew to encompass fields beyond traditional systematics to include cytology, genetics, evolution, developmental morphology, and conservation biology, following the successive historical unfolding and development of these fields of inquiry along most of the 20th century. He made notable contributions to these areas, including the articulation of the polyploid complex; promoting an appreciation of the phenomenon of introgressive hybridization and its pivotal role in understanding evolution; and lending clarity to understanding of phenomena such as apomixis, polyploidy, and hybridization, and their interaction in plant evolution. In addition, he did the most to synthesize the disparate ideas, data, and opinions pertaining to a general theory of evolution in plants that was consistent with a general theory of animal evolution. In fact, more than any other botanist, he was the individual credited with serving as one of the founders of the "Neo-Darwinian," or "synthetic" theory of evolution that accommodated Mendelian genetics within the framework of Darwinian evolution. His major work, *Variation and Evolution in Plants,* which appeared in 1950, synthesized perspectives from a range of disciplines including plant genetics, systematics, population biology, paleobotany, and plant geography and was regarded as a path-breaking work of synthesis, still read widely and cited in the scientific literature (Stebbins, 1950; Solbrig, 1979; Raven, 2000). In addition to earning Stebbins the status of botanical architect of "evolutionary synthesis," it also served to inspire, if not launch, a new area of research known as plant evolutionary biology. The book also placed Stebbins alongside the ranks of major figures associated with 20th-century evolutionary biology such as Theodosius Dobzhansky, Ernst Mayr, George Gaylord Simpson, and Julian Huxley, some of whom were his close friends as well as good colleagues.

In short, his scientific career, which spanned much of the 20th century and engaged a number of new areas, made him an important figure whose reflections on science are interesting to explore in and of themselves, especially for anyone interested in botany, genetics, evolution, or the general history of 20th-century science.

Although the broad overview of his scientific life is missing from *The Ladyslipper and I*, specific research interests are discussed at length, though selectively, as are the varied plant groups that drew his attention as well as their admirers, many of whom were Stebbins' students, colleagues, or friends. As we might expect, plants do figure prominently in this book, and the title of *Ladyslipper and I*, which Stebbins chose in one of his last versions, appropriately thematizes Stebbins' own final retelling of his life. So too, does the inclusion of Stebbins' memories of his interactions with botanists and collectors, and his frequently humorous and colorful travails in finding plant locations. A skilled mountain climber and trekker, Stebbins loved to explore the nooks and crannies of mountains and fields, especially of California, which was his home for most of his adult life. He took frequent advantage of his botanically enriched environment with his family and friends, but also whenever he taught formal university-level courses. A popular teacher whose courses in botany and evolutionary biology at the Berkeley and Davis campuses of the University of California attracted hundreds of undergraduates, Stebbins included extensive field trips as part of the curriculum. He enthusiastically guided treks for keen California botanizers, especially if they were willing to rough it alongside him. It is said of Stebbins that he could accurately determine altitudinal elevation merely by examining the flora, a fact known to his colleagues, students, and

companions on his frequent field trips. One of the most important aspects that emerges in this retelling of his life is just how much the natural history of plant life mattered to him. This autobiography makes possible a renewed appreciation of Stebbins as a naturalist, collector, and indeed a world traveler who appreciated the diversity of plant life not just from an experimental or laboratory setting but from a staggering range of geographic vantage points. He was, after all, a pioneer of conservation efforts in California to preserve the native flora.

A skilled raconteur, Stebbins gives the autobiography a story-telling quality by opening with early memories of childhood experiences growing up in New York, Maine, California, and Colorado. A family of wealth and privilege, the Stebbinses traveled within social channels that offered abundant opportunities for young Ledyard in the way of leisure time, the best of educations, access to the artistic, scientific, and financial elite of American society, and a warm and nurturing environment that fostered his growing interest in natural history. George Stebbins Sr. (for whom Ledyard was named), as this autobiography suggests, was very much the embodiment of the masculine ideal at the time and a figure Ledyard clearly worshipped throughout his life. His stern, yet kindly Edwardian face, in a yellowed photograph, still hangs on the wall of the public library in Seal Harbor, Maine, where the family spent summers. Ledyard's mother, Edith Alden Candler Stebbins, remains a nearly invisible figure in Ledyard's life. His antics with his two siblings, especially his older brother Henry, and the details of their mostly happy childhood with their German governesses, animals, and schoolmates make for one of the more charming portions of this book. Stebbins' later educational experiences at Harvard's renowned but troubled botany department were fairly typical for graduate students at the time, but at his retelling make for an especially colorful depiction of the trials of becoming a botanist at Harvard amidst all the competing egos.

Yet another segment of the autobiography opens a new chapter in the history of genetics by introducing the reader to one of the most renowned departments, and indeed schools, associated with genetics in America, namely the Genetics Department at the University of California, Berkeley. Founded by Ernest B. Babcock, who led it with a vision that linked agricultural practice to genetics, the department in the 1930s and 1940s was a powerhouse of innovation and influence. Stebbins' account of his experiences with distinguished colleagues there serves as one of the first historical sources on that important institution as well as of his growing friendship with the Russian émigré Theodosius Dobzhansky. So too, Stebbins' transition to the UC–Davis campus allows the reader to follow the early but critical phase in the development of what is now regarded as one of the premier locations of plant biology and agriculture in the world. More than any other figure, Stebbins came to represent that campus of the University of California system at a critical time in its history. He served as the first chair of the Genetics Department at Davis and was responsible for building a world-class program. Gaining almost iconic status, Stebbins was featured in a famous portrait of him teaching students about plants in the field that came to represent the Centennial celebrations of the University of California.

Other facts about Stebbins' life emerge in this retelling: his love of music, song, and what he called "silly rhyme and verse," along with his keen interest in politics (he was a dyed-in-the-wool liberal), and his fondness for all the arts, which he shared with his second wife, Barbara Monaghan Stebbins, after they married in Davis in 1958. She was also instrumental in introducing him to the Unitarian Church, which they attended faithfully, and in keeping their homes in Davis and Berkeley the hubs of artistic, literary, and intellectual activity. A private person in some respects, Stebbins reveals little about his own immediate family life here, and the failure of his first marriage to Margaret "Peggy" Goldsborough Chamberlaine is only briefly discussed. His relationship to his children, outside of his hiking expeditions with his son Robert recounted here, remains obscure. The unexpected suicide of his younger son, George, is related only briefly with little in

the way of introduction or reflection. Ledyard remained reluctant to probe into this obviously difficult subject, and references to what was obviously a traumatic event are few and far between in other recollections or memoirs.

At the time of Stebbins' death at the age of 94 in his home in Davis, *The Ladyslipper and I* was the last in a series of autobiographical manuscripts that Ledyard Stebbins had drafted beginning as early as the 1940s. Autobiographical reflection was, in fact, a favored genre for Stebbins, who frequently employed it in his casual lectures, essays, and even manuscripts. A serious attempt at an intellectual autobiography dates back to the early 1940s with a long essay written for the benefit of his father (again demonstrating George Sr.'s formative influence on his son). Titled "The Objectives and Philosophy of an Evolutionist," it was a stunningly original work that included his belief in, and explanation of, the new synthetic theory of evolution. Written with the clarity for which Stebbins became known, it resembled Julian Huxley's own famous work heralding the "modern synthesis" of evolution and included a similar skillful weaving of science, ideology, and worldview in the context of World War II (Huxley, 1942). Sadly, that manuscript has never been published, though an original copy is still in existence.

Other manuscripts that appear to be drafts of his autobiography rewritten over the years remained at the time of his death. Some are in fragments while others include intact chapters or chapters in progress. One version stands out in particular: a carbon copy of a typed manuscript on old "onion skin" paper, which includes several lengthy chapters describing his early life and experiences as a child. It is a delightful rendering of class and privilege at an earlier epoch in American history, and especially so to those interested in Ledyard's early years. There is an especially graphic description of young Ledyard treated by a professional "alienist," or what would now be a psychiatrist, for his celebrated temper tantrums that he began to manifest as early as three years of age. Regrettably, subsequent versions of his autobiography entirely delete or abbreviate these detailed chapters of Ledyard's early life.

At least two other titles were used by Stebbins before the final title of *The Ladyslipper and I*. In a manuscript dated to approximately 1975, Stebbins used the title "Descent from the Ivory Tower." It was subsequently entirely rewritten and substituted with a shorter essay titled "Getting There Is Half the Fun," which was drafted in the mid-1980s and circulated widely to his friends and colleagues in photocopied form (my own copy was dated 1987). In the early 1990s, as his health was giving way, Stebbins completed a manuscript closely resembling the final version and began titling it *The Ladyslipper and I*. By that time, he had been influenced by my work on his biography, and an oral history that I had taken. Curiously, aspects of his life as he retold it began to resemble my own biographical rendering, giving his life the continuity and context only possible in a biographical narrative written by someone else. At times, *The Ladyslipper and I* even echoed the rhythm and transitions of my biographical treatment, going so far as to echo particular phrases or words. In an interesting example of the melding of biography and autobiography, Ledyard began to rethink the context of his own life as his biography developed (Smocovitis, 2007).

His attempt at publishing that manuscript in the 1990s failed, though it did not deter him from revising it and sending it out to his friends for critical reading. As his eyesight was failing, he grew even more desperate to complete the manuscript, finally relying on Rose M. Rutherford, his caregiver, to enter points of clarification or changes he wished to make on a then-electronic version of the manuscript. One of my memories of Ledyard's last days was of his trying to remember names, dates, and places he had visited in an attempt to complete the final version of his manuscript. A final, rough version was indeed delivered to the Missouri Botanical Garden Press in 1999 shortly before his death. Reading what became his final draft, I was interested to see a number of chapters he included toward the end that lapsed completely into the then-contemporary issues in plant molecular biology. Breaking entirely from the narrative thread he had

been weaving up to then, Stebbins launches into an attempt to summarize and critique available understanding on a range of complex subjects. It makes for a fitting ending for someone who could not stand to be too far removed from the current literature in science.

The draft submitted to Missouri Botanical Garden Press was Ledyard Stebbins' final version, but it nonetheless required editorial work, as a number of inconsistencies had been introduced in later drafts. But while edited by three individuals — Victoria C. Hollowell, Eileen P. Duggan, and myself — the published autobiography remains nonetheless a work that speaks clearly with Ledyard's voice. Indeed, reading it once again in the final form included here, one can distinctly hear it retold with Ledyard's crisp, upper-crust New England accent; much as it is written, he always spoke in perfect paragraphs with scarcely a breath taken between them. Here thus, is the very final version of an autobiography by one of the major figures in the history of botanical science whose life is clearly worth retelling.

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Editors' Notes

Ledyard Stebbins presented us with an urbane and literate narrative, weaving threads across both his personal and professional lives. As editors, our intent was to retain his distinctive voice, conversational tone, and storytelling style with minimal intrusion.

Therefore, footnotes were inserted only to clarify names or to provide context about the personalities or literature contemporary to the narrated event. Victoria C. Hollowell and Vassiliki Betty Smocovitis authored most footnotes, and their initials, VCH and VBS, appear accordingly at the end of these footnotes.

Identification of the plant and animal taxa can be found in the Index of Flora and Fauna (page 169). Other scientific terms, people, and notable organizations, places, and events mentioned in the text can be found in the Index except Flora and Fauna (page 163).

As suggested in the Foreword, memory can play tricks after several decades, and the multiple drafts of this autobiography naturally introduced typographical and editing errors. While striving to retain Dr. Stebbins' original intent, we verified details and historic facts and refined unclear passages. A number of people deserve acknowledgement for their assistance in checking these names, dates, and other facts. We are grateful for the contributions toward the book's accurate perspective by the following individuals:

Bridget Carr of the Boston Symphony Orchestra Archives; Robin Carlow of the Harvard University Library Archives; Lesley Bannatyne and Jameson Marvin, Director of Choral Activities, of the Harvard University Music Department; Charlie Melichar of Colgate University; Dr. Bernard Kreger of the Harvard Glee Club Foundation; Dr. Violetta Kotseruba, of the Biosystematics and Cytology Department at Komarov Botanical Institute of the Russian Academy of Sciences in St. Petersburg, Russia; Robert L. Dressler, John F. Pruski, and Tatyana Shulkina of the Missouri Botanical Garden; Ulla McDaniel, Principal Public Events Manager, Dr. Albert J. McNeil, Emeritus Professor of Music, and Dr. D. Kern Holoman, Professor of Music, of the University of California, Davis Music Department; Mary-Claire King, Ph.D., of the University of Washington; and Scott Miller of New Line Theatre in St. Louis.

In California, Rose M. Rutherford and Molly Cate were crucial in assisting Dr. Stebbins with later drafts of the manuscript.

Special appreciation goes to Edy Stebbins Paxman and Robert Stebbins, the children of Ledyard Stebbins.

Line art of *Cypripedium acaule* for chapter titles is courtesy of *Flora of North America*, Editorial Committee, eds. 1993+. Volume 26, Flora of North America North of Mexico, 5+ vols. Oxford Univ. Press, Oxford and New York. Graphics assistance was provided by interns James Allen and Nicole Yaciuk at the Missouri Botanical Garden.

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Victoria C. Hollowell
Vassiliki Betty Smocovitis
Eileen P. Duggan

Preface

A short time ago, two of my closest friends and guides through the wilderness of widowerhood in my late 80s suggested that the title of my autobiography should be "A Botanist and Evolutionist in Search of Answers." Upon hearing this suggestion, my mind wandered as it so often does to a glorious piece of music, Johannes Brahms' *German Requiem*. This requiem is important to me because in one of its movements, the following words are set to exquisite music. I prefer to present it in English, as I once had the honor of singing it, rather than in the original German:

Here on earth we have no continuing place
How beit we seek one to come?

This association was natural and critical, as love of great music has always been an important facet of my character. Furthermore, during the ages from 18 to 20 when I was just beginning my life at Harvard, I had the unique pleasure of joining other students under the guidance of the choral conductor Archibald T. Davison and the great orchestral conductor Sergei Koussevitzky in performing this masterpiece of Brahms.

The following account of my search covers the nearly 70 years that have elapsed since this period of decision and resolve. These years, which span more than two-thirds of the 20th century, coincided with the birth of biology as a unified discipline.

The various subdisciplines of our science became cemented together, inwardly by the DNA-RNA protein code and outwardly by the close association of this code to evolutionary changes in populations guided by natural selection. Their culmination was the conception of the origin of humanity from apes and their relatives, some of whom were nearly or quite human in some respects. Although I did not make any major discoveries, I have been recognized as participating in the major synthesis that provided this cement. The following pages are devoted to explaining how I got this way, who were my predominant companions in this search for knowledge, and what has emerged from it up until the end of the 20th century, 1999.

Introduction

In June 1936, my wife Peggy and I were invited by two professors of English at the University of California, Berkeley, Bertram "Bud" Bronson and his wife Mildred, plus James Caldwell and his wife, Katherine, to spend a weekend with them near Lake Tahoe at Fallen Leaf Lodge. In order to escape the heat of the valley, we left Berkeley before sunrise and arrived about noon. After a sumptuous lunch, we were sitting on the porch basking in the sun and gazing at the sparkling surface of Fallen Leaf Lake below us. Suddenly, Bud asked us all, "What should we do this afternoon?"

The Caldwells had planned to visit with friends at a nearby summer home and Bud and Mildred were planning a short hike up a road to Glen Alpine.

When Peggy said she would like to go with them, Bud asked me, "Ledyard, what do you want to do?"

I replied, "I'm going to climb that mountain," pointing to the steep slopes of a conical peak just in front of us.

"Why do you want to do that?" he asked, looking astonished.

"To look for a plant of which a good friend in Washington wants dried specimens," I answered.

"Well! He must be some friend if you are willing to do that to make him happy."

I smiled and said, "It will make me happy, too. First, I like climbing mountains and second, Dr. Blake, who asked me to collect the specimen for him, is largely responsible for my being here." Dr. Sidney F. Blake had given a favorable recommendation for me to Professor Ernest Babcock, the head of our Genetics Department, under whom I was working as a postdoctoral fellow at the time of the Lake Tahoe trip.

We then all went our separate ways. I found that the 2,000-foot climb up Angora Peak, my first Sierran climb, was about as expected. Near the top on clefts in bare granite ledges, I found my plant and was sure that it was *Haplopappus eximius* (now *Tonestus eximius*), a species known only from the area around the south end of Lake Tahoe. I came back with my trophy, to find the group gathering once again on the porch for cocktails.

Bud asked if I had found my plant, and I showed it to him. He looked at it incredulously. "That scruffy little thing? How could that be important to anybody?"

"Well," I replied, "it is a rare plant known as *Haplopappus* and found only on a few mountains in this particular area."

Bud was much amused so that every time after that, when I met him at the faculty club he, the eminent authority on Elizabethan folklore, greeted me by saying, "Hello Ledyard, how's *Haplopappus*?"

This episode illustrates the most important objectives of my career. The first is curiosity about the intricacies of plant life, to which I was dedicated. I had already decided that I would be following in the footsteps of Charles Darwin with respect to plant life in a new effort to find out the numerous causes of evolution and how they differ from one group of plants to another.

Also, it represents many of the themes that recurred throughout my life. As a botanist, I am used to strange names that appear almost ridiculous to the uninitiated. I was very eager to do favors for other botanists and far from minding a strenuous hike for this purpose, I enjoyed the exhilaration of the hike, the view from a high peak, and seeing the rare plants that grow on it. Furthermore, I made a squash preparation of the chromosomes from the fixation that I had made, and found that it possessed 18 chromosomes

that were similar to each other in size and shape. This was the most primitive chromosomal situation that could be found in a plant belonging to the aster tribe of the aster family. Later on, the chromosome number was found in its nearest relative, *Haplopappus peirsonii*, which grows about 220 miles farther south in the Sierra, and it turned out to be 36 chromosomes, so that the two species are relictual members of the same polyploid complex of which other species have not yet been found or are extinct.

So how did I become so interested in such arcane matters? This story aims both to answer this question and to explain how research in this field led to the success of my career as a scientist.

Chapter 1
Beginnings — Familial, Educational, and Botanical

My father was an upper-crust businessman and my mother was a debutante from New York society, the kind of person whose parents recommended marriage with my father.[1] I spent the first eight years of my life in two localities: Woodmere, Long Island, a suburb of New York not far from the present site of JFK Airport, and Seal Harbor, Maine, a resort designed for the wealthy, near Northeast Harbor and Bar Harbor. These communities border what is now Acadia National Park which, when I was first there, was simply called The Reserve and was used largely for hiking. I don't remember the first season I went to Seal Harbor because I went there in a market basket at the age of six months. I do have early memories of when I was four or five years old.

Let us recall the fanciful "expotition" — A. A. Milne's word for the adventures of Christopher Robin and Winnie the Pooh so fits the spirit of my search for the "Welly Baum." I must explain first that my mother, as was typical of the people in her circle, saw her children in the evenings and the mornings. During the day she put us under the charge of a nurse. The nurse for the three of us — my brother Henry, who was one year older, my sister Marcia, and me — was Louisa Bloss. Louisa was kindly, very German, and eager to teach us her native tongue as well as English. One reason my mother hired her was because she felt that, in order to grow in understanding of our world, all people should know some foreign language. Because a French governess could not be found, she hired Louisa, who had a wonderful personality and, of course, spoke German.

Sunday afternoon was usually the time Louisa took us away from our house and into the forest or to the rocky ledges that surrounded Seal Harbor. This particular Sunday, my curiosity button had been pushed and I wanted to find something I called "Welly Baum." Welly Baum was strictly from my imagination. I was fascinated with the orchid flower known as Ladyslipper,[2] and the Welly Baum had Ladyslippers all over. Other than that, it was just an ordinary little tree that must be in the forest somewhere, or so I imagined. I persuaded my brother, Henry, to come with me. So we sneaked away from Louisa, who was busy caring for Marcia, still in a baby carriage. We ventured into a part of the forest that I hadn't seen before and started looking.

Well, we didn't see very much and started to get a little tired, and Henry said, "I think I know a way out of this forest. We will try to go back to Louisa. Let's go, shall we?"

"No," I replied stubbornly. "I still want to find the Welly Baum."

So Henry left me and did indeed find a way back home, while I continued searching. The search, however, ended in disaster. I stepped into a very wet, boggy spot, got myself

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1. His father, George Stebbins Sr., was born in Cazenovia, New York, and was a real estate developer especially prominent in Seal Harbor, Maine. His mother was a New York socialite named Edith Alden Candler. Her brother, Duncan, was a well-known architect who designed "Erie," the famous summer home of the Rockefellers in Seal Harbor. — VBS

2. North American ladyslippers belong to *Cypripedium* L., Orchidaceae, with more than one species known from Maine. H. A. Gleason and A. Cronquist, *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, 2nd ed., 1991. 850–851. — VCH

saturated, and found a very interesting white flower that I didn't recognize but was clearly not the object of my search. Frustrated and tired, I finally stopped and howled in disappointment and fear, as you might expect a four-year-old to do after his grandiose imaginings had been punctured. I learned later that the white flower that burst my Welly Baum bubble was the Labrador Teaflower,[3] but unfortunately it didn't help at the time.

Henry had found a cousin riding her horse on a nearby road and told her about me. She rode to our home to tell my father. Immediately, my father and several friends got up a search party and started searching in the area where Henry had left me. I was found and brought home. Louisa scrubbed me up, Father gave me a good paddling with his hair brush, and that was that. Here was my curiosity running away with me. It did so frequently. At other times that curiosity was my motivating spirit.

This frustrated "expotition" is my earliest childhood memory. However, an event that happened that same summer provoked my first awareness of belonging to a nation, the United States of America. It was mid-August of 1910 that we saw, steaming up the coast, a huge yacht that Father said was the presidential yacht carrying President William H. Taft. When the yacht got close enough to the entrance of Seal Harbor, a motorboat was lowered to bring to dock-side the President and his aides. Disembarking onto a floating wooden platform, the president and his men walked up a gangplank toward a waiting carriage. President Taft greeted an old lady, the widow of one of Taft's close allies, Mark Hanna, who had a lot to do with him getting nominated and elected. The group drove in her horse-drawn carriage to Mrs. Hanna's home about a mile away. Henry and I noted with glee that the President was so fat that the wooden platform on which he landed sank low enough to get his feet wet. After we got back to our nursery, Henry found the biggest book he could locate, put it under his jersey and strutted about the room piping, "I am President Taft!"

The other feature of life in Seal Harbor was more regular and more connected with my parents. These were the "banner days," always a Sunday, wherein one of the three of us, Marcia, Henry, or I, would spend time alone with our parents in a two-man canoe at Long Pond, about a mile away from our home. This was where Father had courted Mother and so was really sacred to our family. As soon as we were old enough, Father and Mother took us, one at a time, sitting in the middle of the canoe, while Father paddled it up Long Pond, about half a mile of quiet water surrounded by fields and forest. The head of Long Pond was a swamp or bog full of interesting plants. Three were the focus of Father's attention. First was the pitcher plant, a plant in which the leaves have been transformed into traps for unwary mosquitoes and other small insects, one of the well-known and abundant carnivorous plants in that part of Maine.[4]

The second, the sundew, was another carnivorous plant. We could watch this plant actually enveloping the insects unwary enough to land on its leaves, trapped in the sticky substance oozed out by the leaf hairs. These hairs were able to bend in and actually pull out the insides of the mosquito and devour them. We also delighted in touching a leaf and feeling those hairs, powerless to trap our fingers.

These visits to Long Pond were climaxed by our arrival at the narrow inlets separating parts of the bog. Father would stop the canoe, Mother sitting quietly in the stern, telling us to be as quiet as possible, while Father climbed the bank, walked out onto the bog, found the pitcher plant and the sundew, and brought them home for us to look at

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3. Labrador tea referred to *Ledum groenlandicum* Oeder, Ericaceae, noted from bogs. H. A. Gleason and A. Cronquist, *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, 2nd ed., 1991. 202. — VCH

4. The pitcher plant in Maine was probably *Sarracenia purpurea* L., Sarraceniaceae. Several sundew species are possibilities from the genus *Drosera* L., Droseraceae. H. A. Gleason and A. Cronquist, *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, 2nd ed., 1991.152–153. — VCH

more closely. He took only a few of them, not enough to make much difference in the population.

The third plant was the orchid *Pogonia*. Fragile pink flowers with a faint, delicate but sweet odor nodded on a slender stalk about six inches high. Father had first shown this to Mother, so it became a bond of affection between them that we venerated just as they did.

This was one of my early brushes with natural history. A more common contact was the assemblage of trees and shrubs that surrounded our house at Seal Harbor, such as the red spruce, white cedar, and shrubby species of *Viburnum*, plus the meadowsweet of the rose family. These were all plants that I recognized and knew when I was only about seven or eight years old. In addition, Seal Harbor often had days when the weather was foggy. When our usual play on the beach was suspended because of the fog, Father would make the afternoons most pleasant by leading us down to the rugged coast to places where there were tidal pools under the sea cliffs, half a mile away from home. In them lived sea urchins, starfish, and other exciting forms of sea life. One of my earliest memories was of sticking my tiny fingers inside a starfish and having the creature envelope my finger with its tentacles. It never hurt, but they did give me a funny, excited feeling that I quite enjoyed. We often found other forms of sea life at low tide on the wet sandy beach in front of the village, such as clams and small fishes that occasionally could be found in some of the tide pools.

Seal Harbor was the wonderland that awoke me to the diversity of plant and animal life surrounding us, but I never imagined that I would become an expert naturalist and certainly had no inkling that my early childhood would have such an impact on my career choice as I matured. Being a professor of plant biology was the furthest thing from my mind. It wasn't until many years later while at Harvard that I faced the dilemma of choosing a career that fascinated me or one that my father, and particularly my mother, thought was "normal" for a person of my station: the ministry, the law, medicine, or almost any other "prestigious" profession.

All of this "Garden of Eden" was split up mercilessly in the summer of 1914, when I was eight years old and my mother was 38. She was very ill, and the doctor diagnosed what first appeared to be a simple and mild case of bronchitis. She did not get better and after many more visits by the doctor, he eventually diagnosed it as tuberculosis. At that time, tuberculosis was the most feared of diseases because there was no known cure for it. The only thing a victim of it could do to make life easier, and perhaps longer, was to go to a warm, dry climate and be constantly attended by a physician. This meant no more Woodmere, New York, in the winter, but rather a major move to the west. After much deliberation, Father selected Pasadena, California, as the most appropriate place for us to reside while Mother recovered. Consequently, in January of 1915, our family was bundled into the New York Central train to Chicago, then across to the Santa Fe Railway's California Limited, the quickest and most luxurious train to California at that time. We saw the now-tamed West from the car windows, back platform, and from stations like Albuquerque, where long stops enabled us to see the Indians and to buy from them silver ornaments, baskets, and other trinkets that they had made.

Newly arrived in Pasadena, Father had arranged for us to live in a house across the street from a boarding house, La Solana, where we took our meals. The aim here was to free our mother completely from cooking and other housecleaning duties so that she could concentrate on getting as well as possible. My siblings and I traversed two miles to the best private school that Mother and Father could locate, namely Polytechnic Elementary School. It was right across from the institution then called Throop Polytechnic Institute but shortly after that renamed California Institute of Technology (Caltech), which I visited more than once in my later years.

My curiosity was once again aroused by the prospect of having to leave New York and go to Pasadena. I wondered, first, whether the school would have any boys with

whom I could make friends, and second, whether the high mountains rising from the upper end of the city would contain places where I could hike and see something of the diversity of the wildlife I knew would be there. Both of these expectations were partly fulfilled by frequent walks between Pasadena and Eagle Rock, over what was then to a large extent open country rather than the solid suburbia it would become later.

Another example of my curiosity running away with me happened one Saturday when, with our governess Fraulein Isabelle Grunert, affectionately known by us children as "Frilly," we went down to the Arroyo Seco, that flows just west of Pasadena. It was the winter of 1915 and rather wet. This meant that Arroyo Seco had plenty of water with many open pools and a wet, sandy shoreline. This impelled me to search, as I had searched the tide pools in Maine, for animal and insect life. On this particular day, I was attracted to what was, I thought, a most unusual insect. It was fairly large, about an inch and a half long and an inch broad. It looked as if it were carrying its eggs on its back. This was a phenomenon to me. I had to know what the strange insect was, but who could I ask? I didn't know what it was, and I was pretty sure that Frilly, my parents, and siblings didn't know either. So I asked some men who were working in the street. I figured that they must know, as they had probably worked in that area a lot. I led them to the spot where the insect was and pointed to it proudly. I was quite unprepared for their reaction, as they, almost in unison, flung their hands in the air and yelled, "Tarantella! Tarantella! Tarantella!" and rushed away at great speed. I stood there, mouth agape, trying to fathom their strange behavior. I shook my head in bewilderment and slowly went back to join Frilly and my siblings.

I still didn't have any way of finding out more about this discovery of mine. Later on, I found out that the word they were yelling was Italian for tarantula. They were uneducated Italian workmen, and to them, the tarantula is believed to be a very poisonous spider. I eventually did find a name for the animal I saw that day, and it belongs in the true spider family of insects, Theraphosidae. I was happily unaware of its ferocious sting, which was not poisonous but feels like a bolt of lightning and has earned for it the name "lightning bug."

When we came to our adolescent years, Henry and I led lives more separate from our parents, particularly Mother. We had the tendency to be little hellions. I had already shown myself to be the worst one in our family. I was often very trying to dear Louisa Bloss, the nurse of our earlier years. One of my tricks was what in German she called "*will und*" and "*will nicht*," which in English translates as "I want to" and "I don't want to." This was my way of getting attention. How I ever became that way, I don't know, but I was. If Louisa suggested a trip to the beach, Henry and Marcia would be enthusiastic, but when asked I would reply petulantly, "I don't want to go."

And Louisa would say, "All right, you don't have to."

Then I would just go lie down on my bed sulking as they would be rushing around getting ready.

Finally when they said "We're leaving!" I would bawl out, "Don't leave me, I want to go, too!" They dealt with this behavior as best they could, but it certainly didn't endear me to any of the people around me.

During the winter of 1915–1916, my mother's health continued to fail so that she had to be transferred to a sanatorium in Colorado. We children remained in Pasadena under the direct care of our governess, Frilly, but mother asked her mother, my grandmother Marcia Lillian Candler, to come to California to supervise us. During the winter, Grandmother died unexpectedly of digestive problems or perhaps heart trouble. This prompted my father to prevail upon his brother, my Uncle Ben, to come to California and take Grandmother's place as our supervisor. He did this for the next two years, during both the winter in Pasadena and the following summer of 1916 at Seal Harbor. During this period, Henry fit in better than I with our elders, while I was again the fresh, smart, little boy. One incident of this behavior came during a sumptuous Sunday breakfast

served to us at the neighboring boarding house, La Solana. My Uncle Ben, while pouring syrup on his well-buttered and delicious pancakes, remarked, "This is the grub that makes the butter fly!"

"But Ben," I piped out in my shrill voice. "Butterflies aren't made by grubs, but by caterpillars!"

I was, at that time, in the Polytechnic Elementary School, where I suffered repeatedly from bigger and rougher classmates who pushed me around and bossed me unmercifully. As an escape from my plight, I began to collect butterflies and learn about them from a popular book by J. H. and A. B. Comstock. When my fifth-grade teacher asked me to tell the class something about my interests, I delivered the first scientific presentation of my life. It was on the nerve structure of butterfly wings.

My mother's continued failing health precipitated our move to Colorado. In Colorado Springs, Mother was admitted to a sanatorium, as her tuberculosis was getting worse. It was clear that we were going to have to stay in Colorado Springs a long time. This forced Father to make a drastic change in the education of Henry and me. At our birth, Father had pre-enrolled us in a boarding school, St. Paul's in Concord, New Hampshire. Father was a close friend of its principal, so that one of his strongest ambitions was to give us our pre-college education at St. Paul's. However, the distance from New Hampshire to Colorado was so great that he had to give up his hope and find for us a boarding school in Colorado. Furthermore, he felt that because of mother's critical health, it would be much better for us to go to boarding school as soon as possible so that he and mother would be relieved of responsibility for us. Moreover, in 1917, Henry's health became so critical that he had to be moved from Pasadena to Colorado Springs where he also was treated for tuberculosis. Marcia and I remained in Pasadena until the spring of 1917, after which Marcia went to Colorado Springs and I spent a month with my aunts in Cazenovia and later, with Uncle Ben and Father at Seal Harbor. Meanwhile, Father had found a boarding school at Colorado Springs that took boys between the ages of 10 and 15. This was St. Stephen's, under principal Ralph Boothby. In the fall of 1917, mother was desperately ill at the Cragmore Sanatorium in Colorado Springs, Father and Marcia were in a rented house in the center of the city while Henry was declared free of danger from tuberculosis and went with me to St. Stephen's Boarding School. There we stayed, Henry and I, for four years, spending most of the summers with Father and Marcia.

Thus, we embark on one of the most miserable times in my life. I had already come to realize that I would never be popular with other boys, largely because I was very awkward and weak. I was behind from the beginning in growth development, including sexual development when the time came, and I was smaller than most boys my age. I was somewhat uncoordinated and could not even throw a baseball, so I was the last one to be chosen for any athletic team and therefore very low on the totem pole among the boys in the boarding school.

This frustration plus my natural orneriness led me into violent fits of temper, some of which I remember quite clearly. A few of these episodes led to interesting discoveries in natural history. One such incident occurred while I was playing with another boy out in the yard of St. Stephen's. He was treating me as everyone else there did, and I got into my temper and began yelling, "Oh Sanford, I'll get you yet! I'll get you yet!" I rushed over to some rocks, picked one up, ready to hurl it at my antagonist, looked at it to make sure of my grip, and stopped dead. My eyes nearly popped out in surprise, because the surface of the rock was covered with a very distinct impression of what looked like a willow leaf. I immediately went back to the rocky area and discovered that the whole school, located on the side of a bluff, had been carved out of a steep, sloping fossil bed. These fascinating fossils were everywhere. I called this to the attention of my previous

antagonist and he ran and told several other people about it and, lo and behold, a gang of us spent the whole weekend digging fossils from the steep slope in the backyard of St. Stephen's School.

The following summer we had a chance to go to the famous Petrified Forest, located about 50 miles west of Colorado Springs in an area known as Florissant. There we saw stone tree stumps up to three feet high and as much as seven or eight feet in diameter, again giving evidence of a past forest where now there was only open grassland. Later I learned that these were stumps of a species of redwood or *Sequoia* perhaps ancestral to the modern coast redwood of northwestern California. Here again, Colorado Springs broadened my understanding of natural history.

Another incident that stands out in my mind during my time at St. Stephen's was when family friends came out from the East Coast and were invited to our house for lunch. The father of that family, John D. Rockefeller Jr., said, "Henry and Ledyard, why don't you take John and Nelson out. They have brand new cameras and want to take pictures of prairie dogs." So we got Father to drive us out to the place where we knew there were prairie dogs. Both Henry and I were a little skeptical about what pictures they would be able to get, but we all got out of the car and John and Nelson stalked quietly up to the prairie dog dens with the little animals chirping and sitting upright beside the entrance. As soon as the boys got near, the prairie dogs ducked into their dens. Then, each of the two Rockefeller boys sat themselves quietly in front of one of the holes down which a prairie dog had ducked, and waited and waited for as long as any of us could stand. I think it must have been between half an hour to an hour, but no prairie dog was bold enough or kind enough to show its face, even for a Rockefeller.

Chapter 2
At the Bottom of the Prep School Pole

After we finished St. Stephen's School, we were sent to California. In 1919, while we were still in Colorado Springs, Mother had become desperately ill and had to undergo surgery to have one of her lungs collapsed, which was a risk to her life. It was certain that if she did not have the operation she would not survive, because the lung was no longer functional and was infected with tuberculosis bacilli. The hope was that it could be removed before it could infect the good lung. Fortunately, she did survive and, as a semi-invalid, lived to the age of 70.

So, in 1920, Henry and I went to Santa Barbara, California. Through our minister, Father located a school near Santa Barbara run by a Bostonian, Curtis Cate. The Cate School, then known as Santa Barbara School, was a combination of a western-type boarding school, where the boys had to learn how to ride and take care of a horse, and the eastern style, where the education was classical, preparing boys for Harvard and Yale or any other eastern institution as well as, of course, for Stanford.

So, I had four years at Cate School, again at the bottom of the totem pole because of my athletic inferiority. I still couldn't throw a baseball at all. I could ride my horse, Querida, and did enter the horse games they called gymkhana, though even here, my scores were always near the bottom of the heap, something I had become used to.

At Cate School, I was not a happy person. Unfortunately, my nickname from St. Stephen's School had somehow followed me and the kids at Cate took to calling me "Stiggy," after Reverend Stiggins in the Dickens novel *David Copperfield.* Often I would put my arms around Querida and say, "You and I are the only friends I have in the world." I was pretty miserable the whole time I went to Cate. In addition, while I was consistently near the top of the school with respect to grades, I was always second to Henry, whose name was inscribed three successive years on the silver bowl honoring the top scholar of the year.

Another disheartening result of my position was that I never was invited to join with other boys who, during the spring or Easter break, organized long camping trips into the Santa Ynez mountains immediately north of the school. At Colorado Springs, while anticipating our stay in Cate School, I had looked up maps to find the location of the highest mountains in that part of California. They turned out to be the South Coast Range, climaxed by Mount Pinos, about 30 miles south of Bakersfield. While other Cate boys in midwinter were, during breakfast, planning trips for the Easter break, I tried to enter the conversation with the statement, "I want to climb Mount Pinos," which in my shrill voice sounded like the word penis. The outbreak of hilarious laughter from this remark did much to destroy any hope that I might have had to be on one of the spring trips. Instead, another boy, Colin Campbell, who lived on a ranch near Santa Barbara and about 25 miles from the school, invited me to his home for two successive springs.

In spite of my unhappiness at school, I was able to have some happiness in three important areas that would interest me all the rest of my life. First, my solo hiking led to cross-country team activity. Because I didn't always want to ride my horse by myself, I took hikes in the mountains. I took longer and longer trips into those mountains, exploring the canyons. One such excursion was a partial disaster because I found myself in a pasture occupied by several cows and a bull. The cows ignored me, but the bull, who was

not about to let his territory be invaded, bellowed with rage and charged at once. It took me about five seconds to realize that I was in imminent danger. I did the traditional "bolt up a tree" and waited for the bull to stop pawing the ground below and leave. It was a wait of about an hour and a half until they all left to go to the barn, leaving me to shinny down the tree after making quite sure that the bull had gone.

Another bit of good fortune more relevant to our main tale involves the longest hike I had ever taken. I started in the morning right after breakfast at eight o'clock and took a trail that brought me as quickly as possible up to 3,500 feet, to the crest of the ridge of the Santa Ynez Mountains. There I walked along the fire trail atop the ridge until I got to the highest peak (4,600 feet above sea level) and found that with a little bushwhacking, actually quite a lot in some places, I could go down another ridge that landed me in a deep canyon not far from the school. The whole trip was 25 miles and the ascent was from about 200 to 4,600 feet above sea level — quite a jaunt for one day, and without water for most of it, until I got to that canyon. I had just a sandwich for lunch. However, this showed me that I did have endurance that other people did not.

So, when one of the school masters suggested that the whole school have a cross-country run I joined with alacrity, saying to myself, "Well, they may beat me, but I won't be slaughtered as badly as I have been in every other sport." After running about half the distance, I looked around me and found myself more or less alone. I didn't know who was behind and who was ahead, but I continued as fast as I could and circled the open country track the masters had laid out. It was five miles altogether. Finally, I was heading up the approach to the school. When I got up to the masters and the porch, somebody said, "It's Stiggy!" — the horrible nickname, for once not so horrible. "Congratulations, Stiggy," someone said, and I realized that I had won the race. That was the most important athletic triumph I ever had, and it led to me being on the freshman cross-country squad at Harvard.

The second of the three things I had was music. Although I did have lessons in piano, I was a rather poor player but still enjoyed it. I had particularly enjoyed, however, the singing led by a visiting master, and though my voice wasn't good, it was still stronger than most of the others. So I thought, "Well, here's something that I can do also."

Mr. Cate, for lack of anyone better, asked me to play on the piano the tune of a hymn that was part of the daily morning service before classes began. Unfortunately, I made so many mistakes that I earned the opprobrious name "Hymn Bungler." Finally, at the end of the semester, I hit upon an idea. I found a hymn in which the lyrics were, "There is a blessed home beyond this land of woe where trials never come nor tears of sorrow flow." For the boys who had just suffered through a round of final examinations, this was a big hit and I was partially redeemed. However, for the next semester, Mr. Cate found Jack Burnham, who was a much better hymn player than I. Later during that semester, one of the boys discovered a weakness in Jack Burnham's temperament, an abhorrence of snakes. It was decided to make full use of this weakness. Two of the common snakes in the hills near the school were rattlesnakes, which we strictly avoided, and gopher snakes, which looked a little like rattlesnakes except for their narrow heads, slender tail, and lack of rattle. These gopher snakes were completely harmless. This nasty trick in which I participated took place on a day when Jack had ridden to the beach and we knew that he would come back as late as he could and still not miss the dinner bell. During that afternoon, we took all of Jack's clothes out of the top drawer of his bureau and replaced them with a large gopher snake. Shortly before the dinner bell, Jack galloped home to the barn, unsaddled and watered his horse as quickly as he could, and rushed up to his room. He opened his top bureau drawer to grab a quick change of clothing. Feeling not clothing but something smooth, round and wriggling, he looked down and uttering a shriek, rushed out of the room in terror, missing out on dinner completely.

The third bonus of Cate School was a course in natural history taught by Mr. Ralph Hoffman, who was a botanist. He was a man who could combine competence in Latin with a broad training in natural history. Unfortunately, he was killed later when he fell off a cliff in Anacapa, one of the nearby Channel Islands in Santa Barbara.

The situation was that I had gone so far ahead in my studies relative to my lack of physical prowess that father decided that I should have another year in school even though I was ready for Harvard. This meant that during my final year at Cate, I was for the first time at school without my brother, Henry. This also meant taking courses that I would not have otherwise taken, including a course in natural history taught partly by Ralph Hoffman, the person who told me what a genus is and what a species is, but I didn't take it further than that while I was at Cate.

Chapter 3
California, the Grand Canyon, and a Cross-Country Expedition

My stay at Cate School ended with three events that are worth recollecting because of the way in which they fit into both my previous and my later life. The first was a rather unusual mountain climb. A mecca for weekend trips from the school was the cabin it owned in the Santa Ynez Canyon in an area now covered by a reservoir. From the school, we rode our horses up a trail that wound up the slopes of the Santa Ynez Mountains, crossed over its summit, and descended into the canyon and the cabin area. While resting at the summit, just before the descent, I had often looked across the canyon to a much higher summit, about 10 miles north of the Santa Ynez ridge, bearing the name Mount Arido, its gentle slopes reaching a summit of 6,000 feet. Nearly all of the slopes were covered with dense, impenetrable brush, but after looking at them repeatedly I detected narrow streaks of open ground that looked as if they might be pathways to the summit. During my final year, they had tantalized me to the extent that I asked an older student, George Higginson, to join me in an effort to reach the summit from the cabin. At that time, I was pretty much under the care of George, who was ready for Harvard but was spending a year at Cate, guiding some of the boys, including me, in their advanced work. George was skeptical of my plan, but agreed to go along with it. We rode our horses over the Santa Ynez ridge and down to the cabin one Friday afternoon in order to make the attempt the following day. On the way, we stopped at the crest of the Santa Ynez and I showed him my plan. George was not impressed. "From here, distances that look small can actually be very large," he said, "and you should know that we can't go through more than a few hundred yards of chaparral."

I stubbornly replied, "Breaks in the chaparral, which from here look very tiny or are even invisible, nevertheless could be big enough for us to squeeze through without too much trouble."

He then agreed we could give it a try, and so we both set out from the cabin as early as possible on Saturday morning. We clambered up the rocks of a dry side gully for about five miles until we reached a point where it branched into several side gullies. We were then in a quandary, and George believed we were stuck. Nevertheless, a small opening overarched by branches seemed to provide a pathway in the right direction. While George waited, I explored this pathway and found that after a few hundred yards it opened up again and soon afterward, I was at the bottom of an open slope. I called to George, he joined me, and we both climbed up to the summit of an open, breezy ridge. The final few hundred yards to the summit of Mount Arido was an easy and exhilarating jaunt.

We sat in the warm sun and looked about us. Looking southward toward the Santa Ynez ridge, we hardly noticed its crest because behind it was spread the vast expanse of the Pacific Ocean. To our right was a somewhat higher ridge that many Cate School trips had visited during the spring vacation, camping trips to which I was never invited. In the opposite direction was a jumble of slightly lower ridges and peaks ending in the high crest of Mount Pinos. To our left was the Matilija Canyon and above it the Topa Topa ridge, which rose from the Ojai Valley. This view was truly remarkable. We were only 20 or 30 miles from the north end of one of the most densely populated regions of the

United States, that surrounding Los Angeles. In the other direction, we were only 20 miles from the well-known and also well-built-up coast near Santa Barbara. However, from the summit of Mount Arido none of these urban areas was visible. At that time, the air was very clear and we could see 50 miles in all directions, all limited to wild lands and oceans. In spite of these long vistas, urban areas were all hidden by lower mountains so that we felt ourselves completely surrounded by wild lands. Perhaps even now this is still an area that one can visit from the California cities and find oneself entirely away from the congestion with which southern California is now associated.

After a well-earned rest, we made the descent easily. George congratulated me on finding the route that he had judged almost impossible, and I returned to the school feeling that I did, at least, have the faculty for finding my way in little-known country.

My second trip during that spring was suggested by another of the older boys who was aiding with instruction, Don Murchie. In January of 1924, he asked me if I would join him during Easter vacation, a few months away, and travel to the Grand Canyon of Arizona and hike for four days into the canyon. I couldn't think of a better way to spend Easter vacation.

Toward the end of March, we took the train to Grand Canyon Village situated on the south rim of the canyon on the Coconino Plateau. As soon as the train arrived, we had breakfast and made arrangements for lodging and meals, first at the Bright Angel Lodge near the bottom of the canyon directly below us, and for the last of our three nights at Hermit Lodge, situated on another side canyon that descended from the Coconino Plateau about five miles left of the village and the rail terminus.

We then started down the broad, easy, Bright Angel trail. As we descended, we soon found that our horizon was no longer the flat plateau, but a part of the side canyon that descended steeply into the main canyon so that the trail followed it in a long succession of zigzags. From these zigzags we could see how the steep wall was an alternation between vertical precipices of limestone, gray or rusty red in color, and less precipitous slopes of coarse or even rubbly rocky slopes composed of sandstone or shale. Horizontal bands of these different formations were separated from each other by equally horizontal hard strata that from time to time jutted out horizontally and formed the boundaries between the successive formations. Finally, we reached a broad, almost flat area between our side canyon and the main canyon. This is known as the Tonto Platform. Once we had reached this platform and hiked along it before the final descent to the river, we could see that the Grand Canyon is not just a canyon, but a system of canyons. The side canyon down which we had descended is only one among scores of more or less parallel side canyons between which precipitous ridges rise to a height almost equaling that of the rim and appearing to form a very unusual array of almost separate mountains. I know of no other place where such an array of mountains that are 4,000 or more feet high above their base — that is, the Tonto Platform — resemble each other almost precisely with respect to the vertical cliffs and slightly less precipitous slopes that form their sides.

From the Tonto Platform, we descended the precipitous slopes of the inner canyon. Its walls were formed from a totally different kind of rock that had no flat ledges protruding from them but rather a jumble of grayish streaks and convolutions. Finally we reached the Colorado River itself, which is about 4,600 feet below the Coconino Rim. At that time, the river was traversed by a metal bridge, which we crossed just before reaching the Bright Angel Lodge. The descent, which had lasted about five hours, had taken us from a somewhat wintry climate at the rim, to a comfortable balmy climate at the bottom of the canyon. We stayed at the Lodge for two nights so we could spend some time exploring the river banks and their surroundings. We then climbed back to the Tonto Platform and, for the third day of our trip, walked along it to the side canyon on which the Hermit Lodge was located, and up to this lodge for our final night. During this night, the weather cooled noticeably so that when we started our last day it was already reverting to

winter. As we followed the trail up the canyon wall to the Coconino Plateau, the sky became increasingly cloudy and snow began to fall. By the time we reached the rim, we were in a snow flurry so that as we looked back down the trail we saw nothing but a swirl of snow flakes descending into the void. This was a suitable farewell to this extraordinary region that had given us so much pleasure and knowledge.

When I made this trip, I formed memories of scenes that I did not try to explain at that time, because I had little knowledge of geology and the kinds of rock formations that make up the canyon complex. Since then, I have talked with a number of geologists about it and have had formal instruction in geology. The combination of conversation, teaching, and memory blend into and reinforce each other. I mention this because of arguments that I have had with creationists when I maintained, as do other geologists and evolutionists, that the Grand Canyon complex by itself cannot be interpreted in any way except the great age of its various features. The great difference between the rocks that form the inner or lower canyon and those that lie above it from the Tonto Platform upward is fortified by the complete absence of visible fossils in the lower canyon and the succession of fossils, chiefly marine, that exist in the various layers or strata forming the walls of the upper canyons, particularly the side canyons. To me, the jumbled, chaotic metamorphic rock that forms the side walls of the inner canyon resembles the equally jumbled and chaotic rock formations that one can see in parts of Mount Desert Island, Maine, and New England generally. The regular flat layers of limestone and other formations that form the bulk of the upper canyon walls resemble the equal flat or tilted layers of rock with which I had become familiar in central New York when visiting waterfalls in the vicinity of Cazenovia and the neighboring Finger Lakes region. The marine fossils embedded in the limestone just above the Tonto Platform belonged to the lampshells or Brachiopoda that I have also seen in central New York, even in the rocks that form the walls of some buildings. Most impressive is the fact that the fossils embedded in Grand Canyon rocks form a series from more ancient to less ancient strata that runs parallel to similar series in the rocks both of central New York and Midwestern areas like Wisconsin and Minnesota. Consequently, the account given in a 1982 guidebook, *A Field Guide to the Grand Canyon* by Stephen Whitney, is credible to me on the basis of wide experience rather than blind faith in an authority. I shall not discuss further the quarrel between creationists and scientific evolutionists. I mention only that creationists are governed by a faith that they consider sinful to deny, even if observations seem to contradict, while every teacher of science insists that students retain a healthy skepticism and are always ready to reject any theory if it runs counter to actual experience, no matter what the prestige of the author. In the present example, the evidence indicates clearly that the Grand Canyon complex is the result of a succession of uplifts of the earth's surface similar to those that have produced mountain ranges or high plateaus in all parts of the earth during its long history, accompanied by dissection of these highlands by the action of rivers that flow from highlands to the sea. This succession is clearly summarized in Whitney's *Field Guide*. The author's evidence should be clear to anyone who reads the guide carefully and goes to the canyon or similar areas in which the story of the rocks tells us that such long, continued uplifts and erosions have occurred.

My final farewell to Cate at the age of 18 was also in the company of Don Murchie. He very much wanted a companion for a projected motor tour of the United States, starting at Santa Barbara and going up the coast to Monterey, across the state to Yosemite and Tahoe, then to San Francisco and north to Seattle. From there we would drive east through Washington state, across the mountains to Yellowstone, and from there directly east to his home, a suburb of Boston. He bought a Model T Ford and had it modified so that it could negotiate the steep grades that we would encounter along the route. We would camp every night along the way. After getting permission from my parents to

join him, I bubbled with enthusiasm for the project. At that time, paved roads existed only near the large cities so that 90 percent of our traveling was on roads that were only two lanes wide and either unsurfaced or graveled. We left Cate during the last week of June with the back of the car loaded not only with camping gear but extra tires, tire pump, and other equipment for enabling us to survive mild breakdowns, which fortunately did not occur. In 1924, few motorists had been hardy enough to attempt such a long journey.

From Cate and Carpinteria, we drove up the coast and inland through San Luis Obispo, Paso Robles, and King City to Monterey, Pacific Grove, and the 17-Mile Drive at Pebble Beach, where we spent the second night of our journey. The 17-Mile Drive, with its unique Monterey cypresses that assume gnarled and twisted shapes and its granite rocks like those of Mount Desert Island, was the first of a long succession of natural beauty.

The first deviations from the planned route of our trip came after we had driven east over the coast ranges and were about to enter the Central Valley. The route from Hollister to Merced was blocked because Merced County roads were closed due to a ravaging epidemic of hoof-and-mouth disease in cattle. Cars had to skirt around it on dirt roads that were broad enough, but were so bumpy that they aroused all of the rattles of which a Model T Ford was capable. We breathed more easily when we reached the foothills and camped near the small town of Raymond. In late June, the foothills were oven-like and this site was the hottest that we had encountered. Our hopes for cooling off during the night were dashed effectively by a brush fire that almost closed the route for us again but that we bypassed the following morning through guidance from the state Forest Rangers. We then drove up relatively narrow roads until we reached the rim of Yosemite Valley with its view of the majestic valley walls that inevitably filled easterners like ourselves with awe. We camped in an assigned campground from which we radiated outward to see the sites that now have become familiar through several visits. Nevertheless, I am always impressed by such views of Half Dome from Mirror Lake and the same Half Dome in an entirely different aspect from Glacier Point. We lingered for some time among the big trees at Wawona, through one of which we could drive as if through a short tunnel. Finally we left the valley and spent a day of the most difficult driving that either of us had ever faced. At that time, access to the valley was only over one of two one-way roads, Wawona from the south, and Crane Flat from the north. The present principal access road up the Merced River was finished one or two years after our visit. Because of this situation, the Park Service allowed cars to enter the valley on either route at the hours of 7:00 a.m. and 9:00 a.m. and other odd hours throughout the day, and to exit at even number hours such as 8:00 a.m., 10:00 a.m., and so on. To modern travelers, these restrictions of access would be regarded as a boring nuisance. To us, however, it enhanced the feeling that we were truly explorers of long-distance motor trips such as that few others had achieved, particularly in a small car like Henry Ford's Model T.

On our planned day of departure, we lined up for the 8:00 a.m. shift north to Crane Flat as early as we could. After leaving the valley, we could not drive from Crane Flat to Tioga Pass because a road had not yet been built but had to drive down to Aspen Valley near the north end of the park, before we could drive up the grade to its upper and eastern limits. The route upward was narrow, winding and rough with many steep grades. It almost seemed as if for every 100 feet upward we had to drive 50 feet downhill. This was hard on our car because in designing his Model T, Henry Ford did not provide any force except gravity to feed the fuel from the tank in the rear to the engine in the front. This meant that if the level in the tank was too low, the fuel would not feed into the carburetor. Situations like this did not arise on normal roads, but traversing Tioga Pass in 1924 was by no means a normal trip. Although at Aspen Valley we filled our regular tank and a supplemental can, which we carried for emergency, by the time we reached the highest of the

steep grades, we were in the embarrassing position of having the engine higher than the tank and no gravity feed into the carburetor.

We had been warned about this possibility and provided, on paper, two solutions. One was to turn the car around and back up the grade. As we were on a road that was barely wide enough for two cars and was bordered on the left by an abyss-like drop downward and on the right a steep slope up the mountainside, this alternative was impossible. We therefore were forced to use the second and very slow alternative, which was to open the hood, feed gas directly into the carburetor and travel as far as this would take us before repeating the process.

We eventually reached the summit of the grade and descended to Tenaya Lake, another welcome spot where the scenery of the high mountains began. From there, the ascent passed Tuolome Meadow, where we filled up on gas, and on to the summit of Tioga Pass, which was delightfully easy. It was now 6:00 in the evening. We had taken 10 hours to travail 80 miles, the shortest distance per hour that I have ever experienced. Camping was difficult because of the swarms of mosquitoes, but we were so glad to be at rest after our 10-hour ordeal that we both fell asleep quickly.

The next morning, we got off to another good start. Very soon, however, our progress was stopped briefly by another startling event. The highway east of the pass descends through a delightful succession of small lakes, lush meadows, and bubbling streams until it suddenly turns around a sharp corner and almost extends into a yawning abyss, Lee Vining Canyon. We easterners driving gingerly on a road that still had only two lanes and no barriers along its sides, were totally unprepared for this possible plunge into eternity. I have rounded this corner dozens of times since then, but will never forget the awe and trepidation with which we negotiated it the first time. Nevertheless, the expert driving of Don Murchie soon calmed my nerves, and we arrived at the foot of the grade ready to turn northward toward Lake Tahoe. On the way, we filled our larder for the next two days. This seemed like a wise move until we reached a point about 100 miles north, the state line between California and Nevada. There, a special quarantine office had been established to prevent any fresh food from leaving California for Nevada or points east, because of the possible contamination from the areas we had encountered further south where hoof-and-mouth disease was rampant. To the outside world, the state of California was as much feared by cattle raisers as was Merced County with respect to other parts of California. There was no alternative but to either throw out two days' supply of steaks, vegetables, and other delightful things or cook and eat them on the spot or near it. We decided that we would have to go back far enough to find something of greater interest than the sagebrush around us and in that way not waste our food resources. We, therefore, had a half day of visiting the east side of the Sierra accompanied by three luxurious meals. The following day, we crossed a corner of western Nevada with minimal sacrifice to our food and reached Tahoe about noon. We camped at Emerald Bay and, for about a day, enjoyed the exquisite beauty of the lake, which everywhere was blue and unpolluted.

The next part of our journey was near the present site of Interstate 80, which at that time was a two-lane, gravel highway, twisting and turning in conformity with the mountain slopes. It seemed to me that every turn was banked so that our little "Fliver" was leaning outward over the canyon. In addition, Don had a girlfriend living near San Francisco and in his anxiety to reach her, did not spare the accelerator. For the next four hours, I clutched the seat as tightly as I could and hoped for the best. However, we reached San Francisco before dinner time and spent the next two days visiting friends.

We then drove north through the awesome stands of 200- and 300-foot-high redwoods and on to Oregon and Crater Lake. We were charmed with its beauty both as seen from the rim of the ancient crater or caldera of Mount Mazema and from the surface of the lake that we reached by hiking down its slopes and renting a rowboat at the

bottom. We both were amazed by the fact that the lake was of just as blue a color looking into the water from its surface as it was from the rim a thousand feet higher.

From Crater Lake, we drove north to Portland and spent a day near the highway going east through the Columbia Gorge. Continuing farther north, we reached Mount Rainier, where we spent a morning looking at the ocean of alpine flowers and signing up with the guide who regularly took visitors to the summit of the mountain. He was of Swiss origin; we did everything that I learned to do later when climbing in the Alps. We left the timberline road head immediately after lunch and reached a lodge halfway up the mountain in time for dinner. The next morning we got up at 2:00 a.m. in order to negotiate the steepest part of the climb before sunrise while its snow cover was in good condition for our boots and ice axes. Fortunately, we had the very best of weather so that while climbing the upper part of the mountain we could look down at a splendid view of other Cascade peaks, such as Mount Adams and Mount St. Helens. The final 2,000 feet were so strenuous for us greenhorns who had done no previous hiking that summer that we were quite exhausted when we reached the top. Others of our climbing group were equally tired so that only one of them, who, like our guide, had climbed in the Alps, felt like hiking around the crater in order to reach the very highest point, about 100 feet higher than our final goal. The descent was relatively easy and we had no difficulty in reaching our car and driving to Seattle in the late afternoon.

We rested for a day and did some sightseeing in this really beautiful city, then started east on the main highway through Washington and western Montana to Yellowstone Park. The most dramatic part of this highway crossed the Cascades. The road did not have anything like the steep grades and rough roads of Tioga Pass, but it did show us the dramatic transition from the lush coniferous woodlands of the west side of the mountains to the barren sagebrush-covered eastern slope. We had already had some inkling of the abrupt difference in landscape caused by the Cascades, which blocked the ocean winds everywhere from California's Sierra Nevada north to southern Canada, but to me this effect seemed stronger in central Washington than anywhere else. Before reaching Yellowstone, we crossed the northern Rockies near Lewis and Clark's very first exploration route more than 100 years earlier.

After we left Spokane in eastern Washington, the road became as rough and steep as it had been in the California Sierra, but by this time we were better adjusted to these conditions. Nevertheless, I have a strong memory of washing our clothes in a mountain stream so pure and cold that I am sure we managed only a halfhearted job of it. At Yellowstone, we saw the geysers, waterfall, and hot springs plus the wildlife. For us easterners, an amazing sight was the antlered elk quietly grazing on a meadow only a few yards away from us without any fence or other barrier between them and us. Near Yellowstone Lake, a bear stopped us on a stretch of road where he had often been fed and which he regarded as his property. We stopped long enough only to look at him and keep him from approaching our car. We had heard some astounding and bizarre tales from the park rangers warning us to be careful about getting too close. One story that had gone around was of a man who stopped his car along this stretch and tried to persuade the bear to get into his front seat so that he could take a photograph of his wife driving with a bear. Fortunately a ranger arrived in the nick of time to stop this foolhardy and nearly disastrous procedure.

From Yellowstone, we drove directly through eastern Montana, South Dakota, and the Plains states until we reached the Mississippi River, which to us seemed rather tame after what we had encountered in the west. We looped around south of Chicago and across Indiana, Ohio, and western New York to Boston and Don's home in Dedham. By this time, Don and I had realized how different were our outlooks on everything we had seen, and our friendship had become somewhat frayed. I went directly to Seal Harbor so as to get ready for Harvard. I saw very little of Don during our Harvard years.

Chapter 4
Life as a Harvard Freshman

After much preparation of clothes and such, carefully supervised by my mother, I arrived in Cambridge on freshman registration day and began my Harvard career.

First, I found my room in the freshman dormitory, which at that time preceded the house plan instituted about 1928. My room and roommates had been selected for me by Dean Chester Noyes Greenough. He put me in with two preparatory school graduates from Andover Academy. Even when I met them, I was not sure how long I would get along with them. By the middle of the year, I was quite sure that I would not be compatible, particularly after they had left on my desk an anonymous statement telling everyone, including me, what a low opinion they had of me. For my next task on that first day, I went to the hall where freshmen registered and planned out a program of courses for the freshman year.

I did not have any strong commitments, but I had been thinking enough about law school that I decided a major in government would be the proper thing for me to do as an entering freshman. However, the freshman year began a series of events that took me away from the position in which my parents wanted to see me and toward, at first, a sort of a lone wolf adventure in natural history and finally into academia. Interestingly enough, however, it was the musical interest that came from Cate that got me started in that direction.

This is the way it was. Because I had been fascinated by the music we had heard at Cate, I decided that one of the five courses that I would take for breadth of knowledge in my freshman year would be music. Now, I did not know at that time that Harvard offered two beginning courses in music: one, Music Appreciation for those who were not going to be musicians, and the other, Harmony for those who were. My freshman adviser, who didn't know any more than I did about this kind of music, got me into the Harmony course, where I didn't do very well although I did end up with a C. There were a couple of spin-offs, however, that were rather interesting. One of them had to do with a fellow student who was constantly annoying Professor Walter Spaulding by his unorthodox way of harmonizing tunes. The dressing-down talks that he got from Professor Spaulding reminded me of the kind of dressing-down talks that I got from my physics master at Cate, Alernon A. S. Davy. When I was being rather stupid about electrical connections and so on, Mr. Davy would say to me, "I tell you again and again and you do not understand! When you get to college, they will tell you once and expect you to understand it, and that will be that."

Well, what I heard from Music I at Harvard was Professor Spaulding telling Mr. Green: "Mr. Green, I tell you again and again and again. And now when you get out of college into the cold world, just you see." Well, all of us did see, and in the cold world this unorthodox young man composed the popular song "Body and Soul" and arranged the music for several Hollywood movie musicals for which he won four Oscars. He bought a mansion in Beverly Hills, where he spent his retirement days. All this was a little different from what Mr. Davy predicted for me, and Johnny Green's life was a little different from what Walter Spaulding had predicted for him.

The other spin-off from music was that I decided that I would join the Glee Club if I could get in. So I signed up and went to the first few rehearsals. My first experience was so discouraging that I persisted only because of unexpected help from an older member

who was sitting next to me. After a straightforward hymn of thanksgiving, our director, Dr. Archibald Davison, exposed us to a wild one about gypsy dancers that left me completely confused. My kind neighbor remarked, "I see that you are new. If you listen to me carefully, I think that I can help you." He was right. After listening to him several times and practicing by myself, I gained confidence. At every rehearsal I purposely sat next to him and continued to progress. However, one evening I couldn't find my new friend, so I sat down and hoped for the best.

After we had rehearsed the first piece, Dr. Davison went backstage and returned in the company of my friend. He then announced, "Next, we are going to rehearse a piece composed by our friend and member Virgil Thomson." At this time, Thomson was still a graduate student and his name was unknown outside of Harvard. Nevertheless, as he gained renown I was much pleased to discover that the man who had really gotten me started in choral singing later became a nationally known composer who collaborated with Gertrude Stein on the opera *Four Saints in Three Acts*. About 15 years later, I went with my wife to hear him conduct this new composition and was astounded to see that my slim sandy-haired friend had become corpulent and nearly bald. Not surprisingly, I followed his entire career with great interest, although I never met him again.

About a month after rehearsing Virgil Thomson's composition, all of us neophytes had to go through what they called the quartet trials to tell us whether we were good enough singers for the chorus or not. We had to find ourselves a quartet, that is, a first tenor, a second tenor, a baritone, and a bass. The first tenor singers were rather rare and they sort of hired themselves out, as it were, so that was no problem. As for the other two voices, the baritone and the bass, it turned out that I knew Richard P. Dow as a member of the Harmony class and so I asked him if he would join up with me. He said, "Yes, Ledyard. There is Clint McCoy as the baritone, and since you're a second tenor and I'm a bass, all we need is a first tenor and we'll find him easily." I got close to Dick with our intensive training for the quartet trials, which we quietly scraped through. I think Dick did a little better than I, but anyhow, I got in, which was the important thing.

Perhaps the more important thing was that I learned that Dick Dow was interested in natural history, too. He was going to be an entomologist, a student of insects, and so I pursued a friendship with him. We decided that we would change our dormitories for the sophomore year and room together. We also roomed near several musicians who were rather strange but fun and all this got me on a more solid footing. Of course, I wanted Dick to meet my parents. I had already gone to Dick's home in Reading, Massachusetts, and met his parents. So I invited him to Seal Harbor with some qualms because Mother, of course, wanted me to be a typical Harvard society man. She talked about the "Hasty Pudding Club" and the thing they called "Dickie," which you had to be in if you were going to get anywhere in the final clubs and the socially prestigious organizations of Harvard, something I was a long way from doing. The unpopularity that I had among the boys followed me to my freshman year roommates, so I was not likely to ever invite a candidate for a final club to Seal Harbor, nor were such people likely to ever invite me anywhere.

However, Dick Dow was a very calm, humorous, compatible person, and Mother had the perspicacity to realize what he was doing to bring me out of my shell. In addition, he played the piano rather well so that we could sit together on the bench and play pieces arranged for four hands, such as the slow movements of Beethoven's symphonies. So, Mother did meet him cordially. Dick and I did all sorts of things together at Seal Harbor and that was the start of a lifelong friendship.

One of our joint adventures I have since designated as a "barnacle race." Among the most common seashore animals in Maine and elsewhere along the sea coast of North America are barnacles. Although they are related to crabs and other crustaceans, this

relationship is little evident to those who see only the hundreds of animals crowded together as they stick to rocks below tide level or to the walls of tide pools. When the tide is out, all one sees is a mass of thin, conical shells. However, when the tide comes in and the animals are exposed to sea water, each one opens its shell and thrusts out a tiny claw, scooping into its mouth a bit of water containing the microscopic organisms that are its food. One morning when Dick and I rowed in our dory boat out to a series of tide pools on the edge of the harbor, I pointed out to Dick these clusters of animals and we watched them perform. Soon it became evident that every one of the scores of them in the pool had a different rhythm of thrusting out its claws and engulfing the food-rich water. After following the performance of several animals, I could determine a rhythm that was characteristic of each animal and differed from one animal to another even though they were close neighbors. This prompted me to take out of my pocket an Ingersoll dollar watch, which most boys of my age possessed, and count the number of scoops per minute. Dick did likewise and for several hours we pitted our scores against each other to see who could find the most active barnacle. This game was never repeated, but it did give me an idea of variations in populations that I had not gotten at any other time. Doubtless, a scientific study of biodiversity in barnacles relative to their environment would be of great interest, including both comparison of individuals in a single locality and between localities.

During the next few years Dick and I became close friends and visited each other whenever possible. However, during the last part of our lives when I became planted in California and Dick in Florida with the mosquito control group, we could continue our friendship only by correspondence.

My freshman year at Harvard marked the beginning of my transition from my parents' social world based on rank, money, and position in the social register to the culture of academia based on intellectual achievement and a position in the world of the university. Although at that time I gave no thought to a career in academia, later events during my sophomore year at Harvard brought about this major change in my cultural orientation.

Chapter 5
Exploring Mount Desert Island with *Gray's Manual*

So, I came to the end of my freshman year and the question of what I was going to do with the summer between the freshman and the sophomore year. Father always said he did not want either Henry or me to look for summer resort jobs because, he said, "I can support you both, and I think it's very important for you to keep those jobs open for those who really need them." So we were required to submit to the idleness and fun that others of our social position had in the summer resort community of Seal Harbor and neighboring Northeast Harbor.

Well, I was unhappy about the situation. I was a terrible tennis player, no one ever wanted to play with me, and I was not a strong swimmer. No one in my social circle could relate to me through such activities, and I lacked the social graces that would have made me attractive to girls or the girls attractive to me. Then came along yachting. My father presented my brother with a 21-foot sailing yacht. Henry began to take a very active part in the yacht races that were headquartered at Northeast Harbor. At first Henry asked me to crew, but after I had bungled two or three very critical situations I was kicked off the boat. That left me really without any chance to do useful work, so I had to decide on something that would occupy my time and be enjoyable.

I had already gotten a little acquainted with plants and with a small volume, *Flora of Mount Desert Island, Maine*, written by two amateur botanists, E. L. Rand and J. H. Redfield, and published in 1894. I looked around me, in the woods and in the meadows and so on, and thought, "Now, how many of these plants I don't know the names of will I be able to learn during this summer? Will that be something to keep me busy?" I found that I could buy a copy of *Gray's Manual* of the plants of the eastern United States,[1] and so I had that classic at my fingertips as well as the Rand and Redfield. I plunged in and found that this was very much to my liking, running down the identity of plant species using the keys in *Gray's Manual of Botany*, marking marginal notes in Rand and Redfield stating where I found them. It was just like a lot of games that I have enjoyed, and nothing could be more fun. So I kept on and by the end of the summer, I knew the

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1. Asa Gray first published his Manual in 1848 as *A manual of the botany of the Northern United States, from New England to Wisconsin and south to Ohio and Pennsylvania, …* . Edition 2 followed in 1856, *A manual… United States, including Virginia, Kentucky and all East of the Mississippi, …* . Edition 3 appeared in 1862, was the only issue noted as the School and College edition, *Manual… United States, including Virginia, Kentucky, and all east of the Mississippi, …* . Edition 4 quickly followed in 1863, *Manual…* titled similarly to edition 3, with edition 5 in 1867, *Manual… United States, including the district east of the Mississippi and North of North Carolina and Tennessee, …* and edition 6 in 1890, *Manual… Tennessee…* . The seventh edition appeared in 1908 and was the first titled to Gray as *Gray's New Manual of Botany, A Handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada.* This edition was extensively revised by Benjamin Lincoln Robinson and Merritt Lyndon Fernald. The eighth edition in 1950 as *Gray's Manual of Botany* eighth (centennial) edition, *A handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada* was also edited by M. L. Fernald. Stebbins' *Manual* could have been any one of the first seven editions, with Fernald's seventh edition the most recent and available one. F. A. Stafleu and R. S. Cowan, *Taxonomic Literature 2*, 1 (1976): 988–990. — VCH

scientific names, as they were listed in *Gray's Manual of Botany*, of all of the plants within hiking distance of Seal Harbor and a few beyond Mount Desert Island except for the difficult groups, the grasses, the sedges, and ferns.

I bought a book on ferns because it looked as if I could use the same kind of detective work with the keys for the ferns as I could with seed plants, and that proved correct. But for me, the most important feature of the venture that summer involved a professor who was summering in Bar Harbor. Professor Edgar T. Wherry from the University of Pennsylvania was an expert on ferns and that summer introduced me to one very important feature of these plants, that many of them are tied to the rock formations on which they grow. Even if they are in the forest, they are very particular about the nature of the soil on which they grow so that, in any region, including Mount Desert Island, the ferns could be split into two groups: those that love limestone and soils derived from limestone, and those that are acid lovers. On Mount Desert Island, they were practically all acid lovers so that one had to go somewhere else to find the others. I stayed in touch with Professor Wherry until his death some years later, and his influence had a major impact upon my life.

The final event of the summer of 1925 was planned when Dick Dow was with me at Seal Harbor. We had made contact with Clint McCoy, who had been with us for the Glee Club trials. He agreed that a two-week camping trip to the White Mountains of New Hampshire at the end of August and early September would be a fine ending to the vacation and preparation for the sophomore year. We therefore met at Pinkham Notch on the east side of Mount Washington and first hiked up to a lodge north of the mountain summit. On the trip we alternated between staying at lodges, where we could get our meals and stay indoors, and camping in more open shelters and cooking our meals outdoors. When we reached the crest between the summit and the lodge that was our first destination, we found ourselves in an entirely new plant world. Whereas the lower slopes of the Presidential Range supported a spruce-fir forest of which the species were mostly familiar to me from Mount Desert Island, the higher slopes were treeless and supported low hummock or tussock plants that, according to *Gray's Manual*, were typical of arctic and subarctic regions, extending to the high White Mountains at the southern limits of their distribution. These included dwarf willows, subalpine blueberries, and [ericad] genera quite new to me such as *Loiseleuria* and *Diapensia*. There were even a few species that grow nowhere else in the world, only near the summit of Mount Washington, such as *Geum peckii*. These rewarded well the effort we made to reach their habitat. The similarities and contrasts between the plants of coastal Maine and the higher crests of the White Mountains of New Hampshire introduced me to one of the most important problems of plant distribution that has continued to challenge me throughout my life. During the end of the following academic year, when Professor George H. Parker introduced me to Charles Darwin and the problems of evolution, I had ample time to reflect on my experiences in coastal and high alpine plant life, as Darwin did on the evolution of the animals on the Galápagos Islands. We descended from Mount Washington on its southern ridge, known as Boott Spur, notable for supporting only a few species, all of which are widespread in subarctic North America. I had already realized from my course with Ralph Hoffman at Cate and from Dr. Wherry that spore-bearing plants like ferns and club mosses are more primitive than seed-bearing plants, and that cone-bearing seed plants such as spruces and firs are more primitive than those with flowers. I was therefore quite surprised to see that only 10 to 20 percent of the plants on Boott Spur were flower-bearing and these were low, inconspicuous ground-lovers like threeleaf goldthread (*Coptis trifolia*) and a small species of sedge in the genus *Carex*. This remarkable situation would arise in my later study of the evolutionary primitiveness or advancement of plant species as compared to the geological age of the place where they grow.

From the southern end of Mount Washington, we hiked westward to the mountains above Franconia Notch and ended by climbing Mount Moosilauke at the very southwestern corner of the White Mountain region. By this time, we were pretty tired and had been somewhat annoyed by the succession of cloudy and drizzly days so numerous that while we were in the area, we hardly ever saw the sun. We were reminded forcibly that it was time to go back to civilization when we woke up on the final morning and found that our lean-to was surrounded by about two inches of snow, during the first week of September. The trip had nevertheless been highly successful, partly because of the fine companionship that we shared during day after day of dubious to bad weather and also due to the new vistas of plants that had been previously unknown to me.

From the road head below Mount Moosilauke to the nearest railroad station was an easy hike, so that we reached Cambridge refreshed and ready for a new year.

Chapter 6
Botany Trumps Law for the Harvard Sophomore

Dick Dow and I said a temporary good-bye to Clint McCoy, whom we saw again often during the year, and went to the dormitory rooms that we had rented for the next two years. Our companions who had rented rooms in the same suite were an odd lot. Nearest to us in professional interest was Sidney Darlington, an engineering student whose later career was spent entirely with Ma Bell (later called AT&T) where he earned the remarkable distinction of being elected to the National Academy of Sciences, an honor that I also later achieved. Much later when the 50th annual yearbook for our class was published, I determined that Sidney and I were the only members of the 1928 class of Harvard who achieved that distinction.

Three of our dorm group, Henry Clarke, Robert Bates, and W. King Covell, were musicians. Clarke and Bates also were members of the Glee Club, so that we went to rehearsals and concerts together. Henry was the most extroverted of the group and an inveterate jokester. He invented a nickname for the final club socialites and similar classmates, that illustrious group whose company Mother hoped I would attain. This nickname was "pneumatics," short for thermopneumatics, or men full of hot air. King Covell did not enjoy the Glee Club but spent most of his spare time playing J. S. Bach fugues and similar pieces on the nearest available organ or piano. One final member of the group, Lovett Garceau, was the most offbeat of all. He spent all day many weekends sitting in the bathtub, which was equipped with a wooden shelf on which his shaving and washing gear were placed. Henry called it "bathtuba mirabilis," a corruption of the designation of a particular kind of church organ stop. Lovett spent part of his summers in Paris living with his mistress and regaled us with lively but unpublishable stories of their life when he came back.

I am not unhappy at all that so much of my undergraduate life was spent in the company of musicians. In spite of my inability to play an instrument, I enjoyed, both at Harvard and later, intimate knowledge of classical music, particularly string quartets and other chamber music. I recently read a study that seemed to show both composers and scientists perform better when they are acquainted simultaneously with both fields. I myself have found that listening to one of my favorite quartets or sonatas has helped me to solve a scientific problem, and that I have developed close associations between a piece of music and a particular bit of scenery. An example of such associations is the drive from Tioga Pass, the eastern exit from Yosemite National Park into the rim of Lee Vining Canyon, coupled with the introduction to Beethoven's Piano Sonata Opus 110, in which a gentle and lyric introduction is followed by a precipitous descent through a series of arpeggios.

So I went back to Harvard. There I was, still enrolled in government courses and history with Professor Roger Bigelow Merriman, whose nickname among the students was "Frisky" because during his very popular lectures, he almost danced in his energetic walks back and forth across the lecture platform. Through him and his teaching assistant I acquired a background for the literature that I read and for the musical compositions of which I had became so fond. Like other Harvard sophomores, I rarely or never spoke to the famous professors who gave us lectures in a large hall. On the other hand, we had weekly sessions with a teaching assistant, who led us in discussions of what the professor had said, assigned reading, and prepared us for the examinations. The assistant

in Merriman's History I, thinking that he would give me a compliment and learning that I could read French rather easily, gave me an assignment to read from a book by Abbé de Brantôme, a French author contemporary with and similar to Francois Rabelais in his offbeat commentaries.[1] The reading (*La Vie des Dames Galantes*) turned out to be spicy accounts of the pleasures and woes of contemporary youths with their mistresses. In addition, this assistant, whose name I can't recall, pointed out that the best way to learn about the relationship between any famous man, whatever might be his discipline, and his milieu was to remember not his year of birth when he was, as Shakespeare put it, "muling and puking in his nurse's arms," but when he was 50 years old and had either accomplished or was accomplishing the things for which he was most famous. Throughout my life, I have remembered and applied this formula and have been surprised at how often it fits, even with my own career.

I was also taking what was called Biology I. It was not biology as we know it today. Biochemistry didn't exist as a subject for teaching undergraduates, so it was botany taught by Professor Oakes Ames and zoology taught by Professor George Parker. I started with botany, thinking that the systematic botany I had learned during the summer would help me with that course, but I was wrong. The course centered around plant morphology with a little bit of physiology and photosynthesis and with a good deal about the reproductive cycles of the ferns, mosses, and their relatives.

One association of interest was with our teaching assistant Gregory Pincus, who wasn't any more interested in the botany part of Biology I than I was. He was a slender young man with a very bushy mustache and black hair. It was not until afterward that I learned that Gregory Pincus was the first person to demonstrate some characteristics of embryos that would predict which was going to be a boy and which was going to be a girl, and years later made the headlines because of his theory that gave rise to the contraceptive pill.

So I started the year with the courses that I really didn't like at all, but did sneak time in which to learn more systematic botany. I discovered that the New England Botanical Club had monthly meetings, at which Professor Merritt Fernald, who was the hero of systematic botany at Harvard at that time, told about his exciting trip to the Gaspé Peninsula of Canada and neighboring Newfoundland, so I did get much immersed in systematics at that time.

For Christmas vacation, I went to New York, where Mother and Father were staying. Mother had thought she was well enough to spend the winters in New York, but found that this was impossible, as she was still a semi-invalid. They left for North Carolina shortly after Christmas. During the Christmas recess, however, Father took Henry and me to hear two performances of Gilbert and Sullivan operettas, *Pirates of Penzance* and *Iolanthe*, neither of which we had heard before. Father commented as we were leaving, "You two boys were so absorbed in your wild laughter that you did not notice the people around us who were staring at you."

During this same visit, I told Father of my dilemma: Being very curious and wanting to know more about plants, particularly the identity of their distribution, but having to take courses that I didn't like. "Do you think that I could become enough of a lawyer or somebody like that to keep myself alive and then spend my real time the way Rand and Redfield did with plants and plant identification in botany?" I asked.

And Father said, "No. In this competitive world you've got to be one or the other. You have to think it over and decide which you want to be."

Well, I went back to Harvard and during the six weeks between Christmas time and between semester break, I thought about this problem heavily and talked more with

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1. Pierre de Brantôme, Seigneur de Bourdeille or Abbé de Brantôme (ca. 1539–1614) penned *La Vie des Dames Galantes* in the early 16th century. http://www.newadvent.org/cathen/02742a.htm. — VCH

various professors and so on, hoping to clarify my thinking so I could make a decision and choose the course that was best suited to my interest and temperament. After agonizing for several weeks, I made my decision. I wrote Father a letter in February, saying, "Father, I now am sure that if there is a choice, I will have to choose botany."

Father was, I think, a little upset, but he said later when he came up to see me in Cambridge, "Ledyard, if this is what you want to do, go do it. You won't become rich, you will have to take the academic vow of poverty. If you get married and start to have children, I can help you with them because I do want to see my grandchildren, so I'll make a few inquiries." Which he did. He talked to a friend of his, a professor of chemistry, and he talked to the people who were teaching courses that I would have to take, like William H. Weston, Merritt Fernald, and so on. He finally gave his approval, and I made the shift from government and history courses to biology and found friends and acquaintances who were also biology students.

The second half of my sophomore year was taught by Professor G. H. Parker, an animal physiologist and expert on animal color changes, but in his lectures he was the one who introduced me to Darwinian theory. I said to myself, "Charles Darwin must be right. This is the way in which I must go in order to explain all of the fascinating diversity among plants with which I have become acquainted." Nevertheless, I thought, "If Darwin was right, natural selection would not promote change if populations were exposed to the same environment, generation after generation, because the most adapted individuals in each successive generation would be as those in the last generation. Evolution will take place only if a population that is capable of new variation is exposed to a changing environment."

I approached Professor Parker at the end of his next lecture and asked him about this problem. "Wait, Mr. Stebbins," he replied, "until I have finished my lectures on Darwin and evolution." These lectures, which he had written into a book titled *What Evolution Is*, told me that in his opinion, the Darwinian theory had so many weaknesses and flaws that it could not explain evolution and that we had to look for other causes.[2] This answer kept me quiet until I had the chance to take other courses. In this way, I became a lifelong devoted admirer of and adherent to the theory of Charles Darwin. Then came the summer between my sophomore and junior years in 1926.

2. George Howard Parker, *What Evolution Is* (Cambridge: Harvard University Press, 1925). — VBS

Chapter 7
Rock Climbing, Maine Mosses, and the Harvard Glee Club

The first event of scientific interest came in June, when I went to Vermont to see plants adapted to limestone or calcareous soils. The most famous area to see this in Vermont was a place called Smuggler's Notch, where I learned several ferns of the genera *Woodsia* and *Asplenium* that were nowhere else in the part of Maine that I knew, but were abundant in this particular spot. Also abundant were some flowering plants belonging to the mustard family, particularly the genera *Arabis* and *Draba*, and a fern that is not acid loving, but somewhat calcareous loving and mainly occurring north of the U.S. border but dipping into the northeastern states in Vermont. This is the scented woodfern (also fragrant woodfern), *Dryopteris fragrans*. I added the state of Maine to the distribution of this species by finding a very small population on the cliff on Schoodic Peninsula, which is just to the east of Mount Desert Island and not a part of the mountain flora but very close to it.

Another trip during that summer was with Dick Dow, when we went to climb the highest summit in Maine, Mount Katahdin. On the way up, we decided to go by what they called the Chimney Cliff rock-climbing route, which we didn't find very difficult at all. But what was exciting was that right in the middle of the chimney, I saw a few sterile rosettes of a small rockcress that I was sure was not anywhere else in New England. I did not take any plants because there were so few of them, but did take a fruiting stalk that had shed its seeds, and that was enough for Professor Fernald to verify my determination of it as a *Draba fladnizensis*,[1] Arctic draba. Fernald felt that eastern North American plants belonged to the closely related species, *Draba allenii*, that Fernald had himself described in 1934. This marked the most significant part of my summer that year. I came back to Harvard this time as a biology major with an emphasis on botany.

My two remaining years as a Harvard undergraduate, followed by three years of study for the Ph.D. and writing of my doctoral thesis, form the second of three stages of transition between my life under the influence of my parents and the domination of my older brother Henry. They resulted in my changing completely my associations with other Harvard students belonging to my class. The second stage occurred during my junior and senior years, during which I associated almost entirely with Dick Dow and our musical dormitory group and other students who, like me, were preparing for a career in science as research workers or teachers. First, my grade point average shot up, because I was finally doing the thing I wanted to do. This resulted in my graduation from Harvard as a member of the scholastic fraternity Phi Beta Kappa, to which I was elected during my senior year.

The year 1927 was an unfortunate one for me, or so it seemed at the time, but in the long run, a year that added greatly to my understanding of botany. While practicing rock climbing in a suburban area of Boston in preparation for a trip with my brother, Henry, to climb some of the famous rocky summit areas of Europe, particularly the Dolomites,

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1. *Draba fladnizensis* Wulfen in Jacq., Misc. I, 147, 1778, refers to Arctic draba. *Draba allenii* was later described from Quebec, Canada, by Fernald in *Rhodora* 36 (1934): 289–292. — VCH

I very stupidly tried a climb without a rope and fell and cracked a vertebra. With a cracked vertebra, the doctor said that I would have to spend six weeks in a cast at the university infirmary and after that, go to Seal Harbor for a quiet summer around the house and should do no really active hiking at all the rest of that year. So I decided I would do what a botanist can always do if the seed plants are inaccessible for one reason or another, namely work on the spore-bearing organisms, in my case, mosses and mushrooms. So during my whole summer I was confined to our home, Cedar Cliff at Seal Harbor, and learned the mosses of the area, at least a large proportion of them, plus the more conspicuous of the mushroom family. The latter acquisition helped me solve a minor mystery while I was convalescing. One foggy afternoon, my father went down to "jack up" the furnace in order to take the chill off of the second floor. He came back saying, "There is a terrible smell down there. Do you know if anybody has had an accident?"

"No, but I will see if I can find out what's wrong." I went down, smelled the same horrible odor, and tracked it to a small ventilator that was letting in air from the outside. My suspicions became so strong that I went outside and over to the outer side of the ventilator. There I found a strange fungus, the lower part of which looked like the stalk of a mushroom, but the top of which was covered with a sticky substance that had the terrible smell. My book on fungi identified it as the common stinkhorn in English, and in Latin as *Phallus impudicus*. I quickly removed the offending fungus and all of the soil surrounding it that might contain bits of its network of threads or mycelium. Then I told my father about it. After that we had no more trouble.

One of the important spin-offs from my association in the dormitory with musicians was my progress with the Harvard Glee Club, which during my stay at Harvard, carried out some really momentous performances. An arrangement was made between our director, Archibald Davison, and the conductor of the Boston Symphony Orchestra, Sergei Koussevitzky, to perform at Symphony Hall a series of the best known in classic choral and orchestral works. The first of these was Brahms' *German Requiem*. The second, Beethoven's *Missa Solemnis*, and later, with Koussevitzky and just the male chorus, the first U.S. performance of Stravinsky's opera-oratorio *Oedipus Rex*.

I found that the Brahms *German Requiem*, the first of these pieces, was perfect for me because it has both soft and loud parts. The soft parts I could practice slowly to myself, and the loud parts I could bellow out when I was alone on a high mountain summit looking for plants. The *Missa Solemnis* gave me new dimension, namely a knowledge of the Catholic Mass sung in church Latin.

Following the *Missa Solemnis*, there was to me a very interesting choral work, *King David* by Arthur Honegger. To me, the unison passages together with choral passages that were rather modern were a new fascination.

Chapter 8
Weston, Fernald, and Plant Systematics

During my junior year, I learned plant science, both the systematics that I had become familiar with on my own, and Professor William H. Weston's course on fungi and their relatives.

Among the advanced courses that I took during my junior and senior years, two stand out for different reasons. The most enjoyable of these was on the morphology and taxonomy of the lower fungi given by Professor Weston, known by all of the students as "Cap." He was the most relaxed of all of our professors, good humored and full of amusing jokes. He delivered one of his best jokes in a lecture that he gave our botany society after he had paid a visit to Barro Colorado Island, in Gatun Lake in the Panama Canal.

At that time, the director of the American Museum was doing early experiments on what is now a regular technique, that is using a flashlight and a pedal on animal trails so that nocturnal animals would take their own pictures. Weston showed us two slides about which he said, "Here is a fine picture of an ocelot walking away from the camera. Note that it is clearly a male ocelot. This is the picture that the director showed us in Panama. In the next slide, you will see what is obviously the same picture, except that you cannot tell whether it is male or female. I acquired copies of those two pictures and in another lecture about that event, I couldn't help uttering the following ditty: 'Here's to our director, on him life never palls, he takes snapshots of ocelots, and censors out their balls.'"

In Cap Weston's course, when the time came to take the final examination, I was still in the infirmary because of the cracked vertebra. Each of my professors was kind enough to see that someone delivered to me and picked up the examination paper. All of the other botany professors turned over this chore to a teaching assistant, but not Cap Weston. He came to my hospital bed in person, delivered the paper with a smile, and said, "Stebbins, I'm sure that you will knock this one for a row of ascogenous hyphae."[1]

The last two words referred to the technical term in fungi. He used them to express his confidence in my ability to perform well. Naturally I reciprocated by writing a paper that got me an "A" in his course.

The course that was most relevant to my future career was systematic botany with Merritt L. Fernald. This was the taxonomy, identification, and geographic distribution of plants, all of those features of plant life that I had been interested in the past two years and had gotten quite far ahead with them. During my enforced quietude of the summer of 1926,[2] I had learned the more difficult of the groups occurring in the Mount Desert Island flora, namely the grasses and the sedges, and my knowledge of them made quite an impression on Professor Fernald. He therefore suggested that, for the research work that was always a small project done in the senior year, Botany X, I look at the specimens

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1. Ascogenous hyphae represent dikaryotic or binucleate cells that give rise to the asci and ascospores in Ascomycota or sac fungi. These hyphae initially project as small clubs from the ascogonium, perhaps fancifully resembling baseball bats. — VCH

2. Stebbins is referring to a mountain climbing accident that led to his having to rest for the summer of 1926 while he recovered from cracked vertebra. — VBS

that the author of the *Flora of Mount Desert Island*, Edward Lothrop Rand, had collected after he finished his volume in 1894 and see if I could come out with a more complete flora of the area. I was most pleased to do this, and so in the fall of 1927, I took bales of newspaper that contained between the sheets specimens of plants collected by Rand, dating from 1900 to 1905, and looked through them for additions to the flora, of which I found quite a few. By my own explorations, I added a good many species to the flora, so that when I was through I could publish in 1929 my very first botanical paper, "Additions to the Flora of Mount Desert Island, Maine."[3]

At the same time, I had gone so fast with this collection that during the end of the first semester it was finished and I had to think up something for the second semester. Well, it turned out that I had quite a lot of difficulty with identifying specimens belonging to the grass genus *Calamagrostis*. Fernald, therefore, suggested that I spend the spring semester laboratory work on seeing if I could straighten out this little problem in the reedgrasses, *Calamagrostis*, as a supplement to the "Additions to the Flora of Mount Desert Island." What I found was frustrating to say the least. The specimens simply would not arrange themselves or could not be arranged by using the characters that other botanists used for this genus. The specimens couldn't be arranged using characters in publications on the genus into clusters that could be separated from each other and therefore recognized as distinct species. To me they appeared to be a chaotic assemblage of individuals.

This made me realize that systematic botany was still an open field, but at the same time I got a new idea about it by taking simultaneously a course under another professor. Edward C. Jeffrey began his career in plant anatomy and then developed an interest in genetics with its emphasis on the behavior of chromosomes. He spent a great deal of time examining plant chromosomes, and was especially keen on the theory popular at the time that stated that hybridization played a large part in evolutionary change.[4] I found this information was not very kindly accepted by Fernald. In fact, toward the end of my senior year, I knew I wanted to continue with graduate study at Harvard and asked Fernald if I could work with him. He said, "Certainly, why don't you work on *Calamagrostis*?"

"Yes," I replied, "but my experience with *Calamagrostis* has been such that I could do a satisfying job only if I combine traditional systematics work under your direction with the study of chromosome numbers and their significance under the supervision of E. C. Jeffrey." I immediately discovered one of those numerous feuds between professors that were prevalent at Harvard in my time.

Fernald gave me a cold look and said, "Anybody who works with Jeffrey can't work with me." There was no doubt in his mind that mutation and chromosomes were not part of what the sophisticated or traditional systematist should know.

Disappointed and frustrated, I shortly thereafter said good-bye, went down to Professor Jeffrey's laboratory, went up to him and said, "Professor Jeffrey, I have become much interested in systematic botany, but I now feel that systematics must be combined

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3. The paper was published in the journal edited by Fernald, *Rhodora*. See G. L. Stebbins Jr. "Further Additions to the Mt. Desert Flora." *Rhodora* 31 (1929): 81–87. — VBS

4. E. C. Jeffrey was a distinguished plant anatomist who was a strong advocate of Darwinian selection. His interest in genetics was unusual for its rejection of the classical genetics associated with the school of Thomas Hunt Morgan. Instead, he endorsed a view of evolution that focused on hybridization as playing a major role in evolutionary change. He followed closely the work of European botanical geneticists such as J. P. Lotsy, whose book *Evolution by Means of Hybridization* (The Hague: M. Nijoff, 1916) was widely discussed at the time. A cantankerous personality, Jeffrey had difficulties getting on with his colleagues. Oakes Ames, his Harvard colleague, once described him as the "stormy petrel of botany." — VBS

with chromosome studies in order to provide a broader understanding of what we're doing."

"Yes, I agree with you," Jeffrey replied. "Why don't you look at the genus *Antennaria*. So far as I'm concerned, you could work on chromosomes of *Antennaria* with me and on systematics at the Gray herbarium with or without Fernald."

That seemed a good arrangement, and I was pleased to see that Professor Jeffrey, while he didn't like Fernald any better than Fernald liked him, was at least not going to turn me down because of that.

So I was hooked and spent my graduate work with the genus *Antennaria*, of the aster family, commonly known as pussytoes. It is interesting because there are two kinds of populations in different species. In some species, male and female plants are equally common, and the females require pollinating to produce seed. In other species, male plants are rare and the progeny of a female plant are almost all female. Nevertheless, even in these species, occasional hybrids are produced, by crossing females with the rare males of another species. These hybrids are largely sterile, but sometimes produce in their progeny new genotypes that are female and produce only female offspring. There are all-male plants and all-female plants, but there are no plants that have both genders combined in the same plant. Why that should be is still an unanswered question open to speculation, but its consequences for taxonomy are tremendous. If a species has only one sex present, the female sex, then it will produce clones of hundreds of individuals, all of which are very similar to each other, whereas if the species has both sexes it will require cross-pollination and therefore any progeny of this sexual species will be enormously diverse.

There had already been carried out a study of the European and Arctic species of *Antennaria*, namely *Antennaria alpina*, in which the author, a student of Otto Rosenberg in cytology at Stockholm, Sweden, had shown that of the two European species, one of them, *Antennaria dioica*, had both genders or sexes present. The name *dioica* implies that, and apparently they were produced by sexual means, whereas the other one, *alpina*, had almost entirely female plants. So this was the cue that I might find a similar situation in the North American species, which in fact I did.

At this point, it is interesting to note that many years later, about 1950, another Swedish botanist of my generation, Axel Nygren, found that in *Calamagrostis* as in *Antennaria*, asexual reproduction by apomixis is common and is responsible for the taxonomic confusion that had bothered me so much while I was studying the specimens under Fernald's direction. There are more species in North America than in Scandinavia, so that in the eastern American *Antennaria*, there are three species that have both sexes present and a varying number depending on your taxonomy, that have all-female or predominantly female plants present. So this was the start I had with working out the eastern North American *Antennaria*. I emphasize eastern because, as I found later, the situation in the Rocky Mountains and westward was quite different.

Chapter 9
Graduate School, Immersion in *Antennaria*, Europe, and a Whirlwind Romance

So for three years, 1928 to 1931, I buried myself in *Antennaria*. Buried myself, that is, except for maintaining my musical interest. This combination resulted in one day that caused me a lot of trouble. This was the night of the performance of Beethoven's Symphony No. 9 with the Glee Club and the Radcliffe women as the chorus at Symphony Hall on a Saturday in late March. My Saturday schedule at that time was to go to the South Station where I took a suburban train to a particular point that I had identified from the herbarium specimens on campus, knowing *Antennaria* were there, and to walk from the station to another one collecting all the *Antennaria* I could find on the way. In 1928–29, hardly any students, including myself, had cars. Because bus schedules were relatively few, I had to rely on suburban trains to take me to places where *Antennaria* grew and back to Cambridge. This particular Saturday, on which the Ninth Symphony was to be sung in the evening, I maintained my usual collecting schedule except that I found an unusually interesting plant that I had to collect and study carefully. This caused me to miss the train on which I had hoped to return. The next train left so late from the suburban station that I got back to my dorm room with barely enough time to change into my dress clothes and take the streetcar to Symphony Hall, without eating dinner and also without having taken a lunch with me. The frantic apparel change and ride to Symphony Hall were completed in barely enough time for me to enter the concert hall with the rest of the chorus. Nevertheless, the lift that I always got from Beethoven's marvelous music made me forget my troubles and sing the "Ode to Joy" with my usual gusto. When the concert was over, we all received full acclaim, and I spent a long evening in the nearest restaurant.

My graduation from Harvard in the class of 1928 was not accompanied by the usual congratulations from my family, because my mother's illness that caused my father to stay in New York with her, plus my brother Henry's absorption with his medical studies at Johns Hopkins University in Baltimore, left nobody free or interested enough in seeing me graduate.

My graduate years were marked chiefly by the hours that I spent as a teaching assistant in two courses, both of them instructed by Ralph Wetmore. One of them was beginning botany, which gave me most valuable experience in my earliest position at Colgate University. The second was Comparative Anatomy and Morphology of Higher Plants, in which we reviewed research that had been published on the cell structure of the most primitive woody plants. This course whetted my appetite for plant evolution and at the same time put me between quirks of humor from some of the students and the sober attitude of our professor, who was one of the least humorous botanists I ever knew. First, came some terrible puns. Two plant genera that we learned much about were named *Welwitschia* and *Gnetum*. On this basis, a student invented a greeting between instructor and students, which was "Is all *welwitschia*?" and the reply was "I *gnetum*, how I *gnetum*!" Then came instructions from Professor Wetmore about the primitive seed plants of which he gave us microscopic slides accompanied by detailed descriptions. His further instruction was "Draw suggested material" and he did not understand why we thought this was funny.

During the summer of 1930, I went to Europe for a tour, first with fellow graduate students, then at the V International Botanical Congress at Cambridge, England. I went both ways on steamships of the Holland America line that had sailings in which all of the passengers were either university students or faculty members from a large number of U.S. campuses, among them both Yale and Harvard.

On the trip from New York to France, I was determined that I would find some romance. This romance began when my Harvard companion and I spotted two young ladies with whom we decided to become better acquainted. One of them was a chubby, German-speaking girl who was returning to join her parents in Switzerland, and the other, Peggy Chamberlaine, who had been a part-time student of fine arts at Yale.[1] My own companion, Rimo Bacigalupi, started by squiring the Swiss girl, while I became friendly with Peggy. My romance resulted in being so much attracted to each other that by the time the boat docked in France, we had become formally engaged. In my romantic enthusiasm, I did not become realistic about our compatibility, or lack of it, and the consequences until much later.

I left Paris in the company of Rimo Bacigalupi, who remained a good friend until his death in 1996. He spent most of his life in the herbarium at the University of California at Berkeley and his geniality made him a good friend of the entire Berkeley systematic botany community. With him, I visited his father's home village in the Apennine Mountains above the Italian Riviera, and got the most interesting glimpse into the lives of the people who had been his ancestors. I then made a tour of Pisa, Florence, Venice, and Milan, one of the most intensive bits of sightseeing I have ever done. From Milan, I went to Martigny, Switzerland, and met Al Currier, a graduate student in mathematics at Berkeley who was a member of the Harvard mountaineering club. Together we met still another Harvard mountaineering club member, Hassler Whitney, and his bride Brock. The four of us took a short train trip to the southern end of the Bernese Oberland, where we had planned to climb some of the higher peaks with Hassler, an excellent mountaineer, as our guide.

Our center of operations was the Swiss Alpine Club Concordia hut on the edge of the large Aletsch Glacier. We reached the hut at noon, and the following morning started to hike up the Aletsch Glacier to the foot of the Mönch at the usual Alpine hour, 2:00 a.m. Unfortunately, by the time we reached the foot of the mountain, snow had begun to fall and it seemed likely that the climb would not be possible. From this intended starting point, we could hike a few hundred yards to an opening in the mountain, which was the upper terminus of a cog railroad that came up from Grindelwald on the other side of the mountain and a short distance from the Jungfrau, the best-known peak in this part of the Alps. There, we mixed with people who had come up on the railroad in nonclimbing apparel while we in our climbing gear, including ice axes, appeared to be seeing civilization and normal gear for the first time. For two hours, we looked through the plate glass window at the glacier we had hiked and then decided that a quick trip back down the glacier to the hut was our only chance of avoiding being marooned by a snowstorm in the unfamiliar surrounding of the railway terminal. We got back to the hut just in time to avoid being caught in a blizzard. We and several other climbers were isolated in the hut for two days while the storm raged around us. We four and other climbers of Swiss origin passed the time by playing cards. We played the usual American "Hearts" while the Swiss played some game that I didn't recognize. The amusement of their game to me was the fact that two of the players were charming girls from the French part of Switzerland, while their protagonists were young men from a German-speaking canton. Although they knew each other's language well enough to converse, playing cards was a different matter. The German-speaking men had to teach the right

1. Margaret Goldsborough Chamberlaine. — VBS

words to the French girls. One amusing difficulty came up because the Swiss German (Schweizerdeutsch) dialect was unfamiliar to the girls and they got mixed up in using the numbers. The number 20 in German, *zwanzig*, was pronounced in such a way that the French girls thought it was "swanski," and it was the same way with *dreißig* ("dryski"), and *vierzig* ("veerski") and so on. Both sides went into gales of laughter at this corruption. One of the German-speaking men asked me to give an account of ourselves that he could put into the diary of his trip. He later sent me a letter from his home in the city of Konstanz that included a publication of his account in the town's local newspaper.

After the storm had finally ended, Hassler tried to guide us on an ascent of the Gletscherhorn, but we found so much new snow lying on our footholds and handholds that we had to turn back from halfway up the mountain. As it was clear to us that the weather would make it impossible for us to do any significant climbing, we ascended from the hut and went our separate ways.

I went on to Zermatt, found a guide and did three conventional climbs. The guide liked my climbing style well enough that he asked if he could take me up the Matterhorn, but his fee was beyond my budget. I therefore went on to Munich, Germany, and from there, to England.

The International Botanical Congress in 1930 was my first introduction to a meeting of many botanists from all countries and of various disciplines. I first went to the sessions on nomenclature but found myself bored and frustrated by supposedly intelligent scientists acting as if they were politicians deciding the fate of botany, when all that interested them was choosing between various alternative scientific names of genera and species. I then went to the sessions on chromosomes, which I found much more interesting. Much of what I heard was familiar through my extensive reading at Harvard, but the personalities of men like C. D. Darlington, who was becoming an oracle because of his forthcoming book, *Recent Advances in Cytology*, and women like Irene Manton, who was just finishing her Ph.D. with a survey of the chromosomes in the mustard family, attracted me greatly, even though Darlington's theory appeared to me to be not well founded. At the very end of the session, there came to the podium a large man with a broad Michigan accent who spoke about the characteristics and chromosomes of *Iris* species that were known to me plus fascinating research in the genus *Tradescantia*. This was Edgar Anderson. At the end of the session, I went up and introduced myself, and he immediately invited me to spend an evening with him. This was one of the most rewarding evenings of my scientific life. He had pithy comments on some of the speakers such as, "The trouble with Darlington is that due to the death of Newton (a cytologist under whom Darlington began his research), he came up too fast and now expects everyone to agree that his ideas are new and modern. You, as a young man, should get acquainted with your contemporaries like Irene Manton and authorities such as Agnes Arber."

During the rest of the Congress, we saw quite a lot of each other and planned to meet again when we were back in the United States. I also spoke to Dr. Otto Rosenberg, who had published with his student H. O. Juel the story about *Antennaria*, which I had read. I also spoke briefly with Georg Tischler, who had published a widely accepted work on geographic distribution and chromosome numbers of the European flora.

The rest of my European trip was spent with my family, who were spending the summer in northern England, where I met them, and afterward in London and in northern France. I got home just in time to finish my third year of graduate study and prepare for my final examination.

Two events of great importance took place during the spring of 1931. First, through Professor E. C. Jeffrey, I received a letter from Colgate University in Hamilton, New York, that I had been appointed Instructor in Biology beginning the following September. As 1931 was the middle of the Great Depression, the news that I would not have to search for a position was really welcome.

The second event was the award of my Ph.D. in Biology that I had thought would be a routine examination of both my thesis and general knowledge and that I would sail through without difficulty. With respect to the latter prediction, I proved to be mistaken. Harvard at that time required only the thesis plus an oral examination that was ostensibly a defense of the thesis but also had become an estimate of the candidate's competence to do research and teach in the field of his thesis, in my case the botany of higher plants. I handed my completed thesis to Professor Jeffrey about a month before the required date, expecting that it would be accepted with little or no demand for revision. I was unprepared for the reaction I received.

In addition to Professor E. C. Jeffrey, the two other faculty reviewers of the thesis were Professors Merritt Fernald and Karl Sax. Fernald apparently signed it without comment, as he knew I was highly regarded by the faculty and didn't want to raise trouble. Professor Sax, on the other hand, had been on the faculty for only a few years, was an expert in the most recent facts and concepts of chromosome cytology, and was very conscientious in seeing that they were reported and interpreted correctly. Thus, two weeks before the expected date of my oral examination, he asked me to come to his office and bring with me a microscopic slide that illustrated the dimorphic sex chromosomes that I had described, accompanied by a review of the entire literature on sex chromosomes in plants of which only a few examples were known.

When I went to his office, he asked me to find on the slide I presented the meiotic cell in which I found these chromosomes. I put the slide under the highest power of the brand-new binocular stereoscopic microscope that Dr. Sax used regularly. Such microscopes did not exist in Professor Jeffrey's laboratory, as his conservative pinch-penny nature had caused him to feel that for such as us, the monocular compound microscope was good enough. Upon examining the slide, my eyes almost popped out. From this new viewpoint, I clearly saw that what I had thought to be two chromosomes of different sizes hitched together end to end were actually, in this nucleus that had not been squashed in accordance with Jeffrey's disbelief in the squash technique, were actually two similar chromosomes, one of them viewed horizontally and the other vertically so that only the spectroscopic view could determine its length. As I had spent many hours searching for other examples of heteromorphic chromosomes, I was quite sure that they did not exist in the species of *Antennaria* that I was studying.

This was quite a shock to Professor Sax and to me. He told me that because I had not properly recognized heteromorphic chromosomes, the 20 pages or so of discussion about them would have to be deleted from my thesis. He also took exception to some of my remarks about polyploidy, in which I had followed C. D. Darlington. "If you should publish a paper on your thesis containing this material," Sax said, "the most progressive cytologists would take exception to it, and your name would become associated with Professor Jeffrey's unacceptable theories about mutation and hybridization."

This remark led me to accept his criticisms and go to Professor Jeffrey and ask him if I could make the changes in accordance with Karl Sax's ideas. This aroused Jeffrey's ire. He pinned me with a cold stare and said, "I will not have a graduate student who is unwilling to stand up for his rights. If you make these corrections, I will not sign the thesis."

I left Jeffrey's office in despair. Here I was, with a job promised as soon as the thesis was signed and expecting to be married to Peggy in two weeks. However, my despondency wore off during the night so that the next morning I went to Ralph Wetmore, who had shown his satisfaction with my performance as a teaching assistant, and asked him what I should do. He asked for my thesis, which I gave to him with trepidation and hope. That afternoon, from my little cubbyhole just outside of Jeffrey's office, I saw Professor Oakes Ames, the gaunt aristocratic chairman of the department, passing by on the way to Jeffrey's office, with my thesis under his arm.

What went on within the sanctum sanctorum, which was separated from me by a thick wall, I could not exactly determine. I could, however, recognize the slow, stentorian tones of Professor Ames' voice, punctuated by the increasingly penetrating and angry yet unintelligible comments of Professor Jeffrey. Finally, Ames left, the door was savagely hurled shut behind him, and nobody saw Jeffrey for the next two days. Nevertheless, Professor Wetmore was able to show me the thesis bearing Jeffrey's signature.

Of the actors in this drama, I had no occasion to see Professor Ames again. Ralph Wetmore and I continued to be close friends, and I congratulated him a few years later on being elected to the National Academy of Sciences and visited him in Cambridge after he retired. After my thesis had been signed by everyone and was safely deposited in the Harvard library with changes made and the pages discussing heteromorphic sex chromosomes sealed together, I broke off my relationship with Professor Jeffrey and mentioned him as my major professor only when I had to.[2]

The following year when I was established at Colgate, I had very useful correspondence with Karl Sax and discussed cytology with him whenever we were together at a symposium or national meeting. As I started my family that same year, every time that Sax met me he asked me not "How is your family?" but "How is your experiment in applied eugenics?"

Because I had now become a cause celebré and was still highly regarded throughout the department, I studied painstakingly for the oral examination that I took shortly after the thesis incident and passed it with flying colors. Professor William J. Crozier, the general physiologist whom I feared most as an inquisitor, told me at the end, "I don't think I remember any other student who appeared to enjoy his examination as much as you seemed to do."

Two years later, Edgar Anderson visited me at Colgate and I related to him the now well-known story "How Stebbins got his Ph.D."

Anderson replied, "When I was a graduate student at Harvard, this story came to me about Charles Eliot, the eminent president of Harvard at the turn of the century. After being made to arbitrate a violent dispute between two botanists on his faculty, he apparently remarked in amazement, "I wonder what it is about the study of plants that make men hate each other so?"[3]

This succession of events closed my career of seven years at Harvard.

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2. Archival correspondence between Stebbins and Jeffrey well into the 1930s suggests that the relationship was severed well after Stebbins left Harvard, if at all. — VBS

3. This notorious statement circulated among botanists for much of the 20th century and beyond. Other sources point to President A. Laurence Lowell as the source of the observation instead of Eliot. None of the original sources have been substantiated so that the quotation must remain a kind of urban legend in the community of American botanists. — VBS

Chapter 10
From Student to Professor

The next four years marked my transition from academic life as a Harvard student to my later life as research worker, instructor, and professor in the University of California system. These four years were spent as instructor of biology at Colgate University in Hamilton, New York. For me, it was the most unpleasant part of my career, but nevertheless served the valuable purpose of training me as a teacher under the influence of an expert in teaching, Clarence W. Young.

Also during that time, I became the father of two children. Hamilton, New York, is only 20 miles away from my father's home town of Cazenovia, so that I often visited my aunts who lived there and invited my Uncle Ben to go to Colgate's locally renowned football games. On the other hand, Colgate and my busy life there kept me completely away from my immediate family. During vacations, I either stayed in Hamilton or went to the home of my wife Peggy and did not see my brother, Henry, at all, because he was very busy at medical school in Baltimore.

At the time, Colgate was for men only and those with great aspirations. It hoped to enroll an Ivy League student body and at the same time have a powerful winning football team. My responsibilities were two: First, teaching two sections of about 30 students each in a survey course required for all lower division students, and second, teaching all courses in botany. For the botanical courses, I had neither teaching assistants nor technicians. For the laboratory work, I set up all the equipment myself; attended to the questions of all the students, which fortunately were not very many; made out and corrected all examinations; and at the end, put everything away. For the survey course, I was one of three instructors under the direction of Clarence Young, a psychologist who had a Ph.D. from Stanford and did research in the traditional aspects of his field. Nevertheless, his course was very well organized so that teaching it greatly broadened my knowledge of psychology. Clare and I became close friends and together finished in 1934 a book containing the material of our survey course, which was chiefly human anatomy, physiology, and general principles of biogeography, genetics, evolution, and similar fields. Clare gave the book the title *The Organism and the World of Life*, but as I could visualize many students eliminating two letters from the middle of organism, I insisted it be called *The Human Organism and the World of Life*. It was published by Harper and Brothers and during the 1940s was adopted by other universities similar to Colgate around the country. It was also adopted by the Armed Forces as a required course for teaching draftees and GIs during World War II.

Naturally, these assignments kept me very busy during all regular workday hours. Nevertheless, I did have time for research during weekends, holidays, and the summers. For the first year, I borrowed specimens of *Antennaria* in order to attack a problem left over from my thesis, the occurrence of male plants in a widespread species *Antennaria neodioica*. To my surprise, one of the specimens borrowed was collected in the Shenandoah Valley of Virginia, and contained plants much smaller than any others, several of which were males. As I had already made friends with Dr. Sidney F. Blake, the taxonomist at the Department of Agriculture in Washington who was a specialist on the family Asteraceae to which *Antennaria* belongs, I sent him the locality as was written on the specimens label and asked him if he could take me from Washington to the locality. He

replied that he would be delighted to do so and that the spring vacation I suggested would be ideal.

In the spring of 1932, Peggy and I were invited by her mother to the Chamberlaine home in Baltimore, and from there we visited the family home in which Mrs. Chamberlaine grew up in Warrenton, Virginia. This gave me a fine chance to go to Dr. Blake's office and ride with him to the *Antennaria* locality on Massanutten Mountain, to the west of the Shenandoah Valley. Seeing the living plants in abundance, I could be sure that male and female plants were present in equal numbers. I also observed differences in form as well as size among all of the plants in this locality, and all of the female plants that were exclusively present farther north. I eventually, in 1935, grouped the Massanutten Mountain plants with others found in Virginia, West Virginia, and southwestern Pennsylvania into a newly described species, *Antennaria virginica*, which differs from the northern *A. neodioica* in possessing male and female plants in equal numbers and in the smaller size of all of its parts. This was the first new species that I described in my career.

The distribution of *Antennaria virginica*, along with several other highly distinctive species in eastern North America, is almost entirely restricted to shales of Devonian age. So, from 1932 to 1935, Peggy and I made several more trips to the area so that we could visit with relatives and I could learn more about my new species.

A spin-off from my teaching was a summer course in field botany that I asked to introduce during the summer of 1933. Because there was no formal extension division at Colgate, the administration agreed that I could ask the students to pay their way and, in turn, receive three units of credit for a two-week trip. I opted to visit with them the Bruce Peninsula in northwestern Ontario, which sticks out between Lake Huron and Georgian Bay in Canada. We had an easy two-day drive to the peninsula and camped on the shore of Lake Huron. I then explained to them what Professor Fernald had told me — that the Bruce Peninsula was high enough to stand up as a nunatak above the ice of the glacial age and to conserve a relictual ancient flora, which we hoped to find.[1]

So the next day we drove to the foot of a limestone cliff rising above Georgian Bay, the top of which is the highest point on the peninsula. As we were climbing the steep slope beside the cliff, one of the students picked up a pebble and asked me, "Isn't that granite?" When I replied that it was, he asked, "Where did it come from?"

"Almost certainly from the other side of Georgian Bay, which is the edge of the Laurentian Shield that contains a lot of granite and other igneous rocks," I replied. "But there were four glaciations in this area and it's possible that this pebble was carried here by an earlier glaciation."

"Well," said the student, "I have taken geology with Professor Root. He said that you can determine the age by striking the pebble a hard blow. If it disintegrates, it is ancient, but if it does not, it is recent."[2]

I took out my plant digger and struck it hard against the pebble. It remained intact and bounced over the cliff. Naturally, my face went very red. It became redder still when we failed to find interesting plants on top of this bluff and redder yet when we returned to the car and drove over the neighboring terrain, seeing one large boulder after another of igneous rock sitting on top of limestone. Nevertheless, we found a sufficiently large

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1. A nunatak is a mountaintop not covered by ice and generally protrudes out of a surrounding glacier. Earlier in the 20th century, Fernald had proposed the "nunatak theory" as a way of explaining relictual populations of plants that remained unaltered as the ice sheets receded during the Pleistocene. — VBS

2. Towner Bowditch Root, M.S., was an associate professor of geology at Colgate. — EPD

number of rare plants from that day's experience to keep our interest up and continue the exploration of the peninsula.

After we had returned home, I pondered this problem, realizing that Professor Fernald must have given me mistaken information. I knew that one of the Canadian geologists that Fernald frequently consulted was so much taken with his idea that northeastern Canada contains many nunataks that rose above the Pleistocene glaciation and that he had become uncritical in evaluating the evidence for presence or lack of glaciation in a particular area. On the other hand, an entomologist, Philip Darlington, brother of my Harvard friend Sidney, in accounting for some rare species of beetles found in the region around the Great Lakes, pointed out that during and shortly after the height of the last glaciation, there were islands of forest between what are now the dry plains east of the Rockies and west of the Great Lakes. Insects and plants that require some moisture could have migrated eastward from the Rockies, where now the heat and drought make this impossible. I later acquired evidence of this through my experiences in California.

Chapter 11
Percy Saunders and Other Colgate Adventures

My four years at Colgate were greatly brightened by events that occurred 20 miles away in collaboration with A. Percy Saunders, a chemistry professor at Hamilton College in the town of Clinton. He was more like the prototype of a Renaissance man than anybody else whom I ever met. Although he was officially a professor of chemistry, his heart and soul were elsewhere. He spent much time with his students, who affectionately called him "Stink" because of his official duties. He also played chamber music, chiefly as first violin in an amateur string quartet. He was a part-time horticulturist and plant breeder with a particular interest in peonies, of which he had a unique collection of species, varieties, and hybrids.

His horticultural interest came from association with his father, a noted Canadian plant breeder who was responsible for a wheat variety, 'Marquis,' that pushed Canadian wheat cultivation several degrees of latitude north of its previous limits.

I became associated with Percy as a result of a conversation during the summer of 1931 at Seal Harbor. Peggy and I had just returned from our honeymoon and were given a reception by Mother in order to introduce us to various friends. One of them, on finding out where we were going to be the following winter, asked me if I knew Professor Saunders at Hamilton College in Clinton, New York. When I said no, she said that she would write him immediately. As a result, we received an invitation from Dr. Saunders soon after we had arrived in the town of Hamilton to begin my teaching at Colgate, and so went to nearby Clinton and were cordially received by him and Mrs. Saunders. The names here are very confusing, but stated briefly, Colgate University where I taught is at the town of Hamilton, while Hamilton College where Dr. Saunders taught is 20 miles away in Clinton.

Dinner at the Saunders home proved to be an unforgettable experience. He greeted us in a velveteen jacket, beaming amiably through every fiber of his generous mustache and beard. We then engaged in a short conversation, which included his question, "What do you know about peonies and their chromosomes?" When I expressed enthusiasm, he said, "We'll talk about that later," and invited the company to dinner.

The dinner was notable to me because of the tossing of the salad over which Saunders presided with rare éclat, shaking into it one after another condiments and oils, which produced a delightful result I still remember. At other dinners, he invited the three other members of his string quartet, and I had my first experience with the quartets of Beethoven and Schubert, played by experts simply for the enjoyment of themselves and their friends.

On another visit, Saunders showed me his garden of peonies. I had known previously only the large pom varieties, which were too far in the realm of cultigens to be of interest to me. His collection was very different. Many of them were direct descendants of native *Paeonia* species of which seeds had been collected in their home areas, and Saunders had received from a variety of sources. Nearly all of them were of the type called "singles" that bear only one whorl of petals enclosing a large number of stamens and three to five carpels. After receiving these species, he had made a large series of crosses between species, which also had a small number of petals and a large number of stamens. Before I came, he had received help in studying them from a botanist, G. C. Hicks, who had received his Ph.D. from E. C. Jeffrey at Harvard, gone to the

University of Buffalo, and unfortunately died as a young man a few years before I went to Colgate. Using Jeffrey's technique of embedding buds in celloidin and sectioning them with a microtome, he had determined the size of buds at which the reduction division, or meiosis, occurs in the formation of pollen grains and verified the presence at that stage of five pairs of large chromosomes. Saunders had been told by others about the superiority of the "squash method" for investigating meiosis, which I approved heartily, so that both of us spent many evenings in the basement of his home, squashing out stamens that had been gathered the previous day. Both of us had to greet our wives with stained and smelly fingers, which they eventually tolerated. For us, those evening sessions of making squash preparations provided unparalleled opportunities for getting acquainted. When we started looking at meiosis in his *Paeonia* hybrids, excitement mounted as we found one after another unusual deviations from the way in which the chromosomes paired in the parental species.

During the summer of 1932, we went together to the VI International Congress of Genetics held 65 miles away at Cornell University in Ithaca.[1] This Congress itself was an exciting experience that regaled us with some of the most important recent discoveries in our field. For instance, a violent argument occurred between the English cytologist, Cyril D. Darlington, and the American Karl Sax, my friend and professor from Harvard. The question involved the timing of splitting individual chromosomes belonging to the male and female parent and the relation of the splitting to the intimate pairing between corresponding maternal and paternal chromosomes that makes possible the recombination of genes via the meiotic phenomena of cross-over. I became amused by the fact that just as this discussion had reached its height, two dogs that had entered the lecture hall through an open door engaged in their own growling and yapping dogfight.

Even more interesting was a presentation by Barbara McClintock, then a recent Ph.D. from Cornell (1927), on meiotic pairing of chromosomes in hybrids between varieties of maize (corn, or *Zea mays*) that differed with respect to genetically determined sequences of genes on the chromosomes. Two dramatically different configurations of chromosomes were determined, one of them in hybrids between parents that differed from each other with respect to the position of the sequence of chromosomes bearing different numbers according to the centromere or kinetochore, and the other between sequences belonging to the same chromosome pair as to homology and bearing the same number as determined by their centromere. The difference was that the particular sequence involved had become inverted with respect to the rest of the chromosomes. These two kinds of differences were little known to most geneticists in 1932, but later, bearing the terms translocations and inversions, were discovered in the salivary chromosomes of the fruitfly *Drosophila* and were illustrated in all genetics textbooks and many biology textbooks. What we saw in McClintock's excellent demonstration was a large cross formed by the two pairs on nonhomologous chromosomes between which a translocation had been found, and a ring or loop that we found in hybrids between two varieties in which a single homologous pair differed with respect to an inversion. The lecture was supplemented by a laboratory demonstration in a different session in which we could easily see and understand what she had presented. Those of us who were interested in cytogenetics became much impressed by the intensity of this woman genius and followed her career step by step. After she retired and shortly before her death in 1992, she became the first woman geneticist to receive a Nobel Prize.

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1. The VI International Congress of Genetics in 1932 is generally regarded as a pivotal moment in the history of modern genetics. It drew to the United States the outstanding geneticists in the world at the time. It also included a number of evolutionists who shortly forged the evolutionary synthesis. In a famous photograph of the members of the Congress, Saunders is photographed next to Stebbins. — VBS

After seeing McClintock's preparations of meiosis in corn, I went back to my lab and looked at the preparations of meiosis in *Paeonia* that had been made by Hicks and loaned to me by Saunders. In several hybrids I saw configurations comparable to those of McClintock, but the peony material obviously lacked one of the principal advantages that McClintock had shown us in corn. She was able in both kinds of hybrids to show the intimate pairing of the very much extended threadlike chromosomes in the pachytene stage of prophase in meiosis I. The slides of Hicks showed that at early stages the chromosomes were too mixed up for me to distinguish individually, and so I could not duplicate her pictures of these early stages at all. The squash preparations that Saunders and I had begun to make showed with equal clarity that this method was no better than sectioning to illustrate the early stages, but that the squashed later stages were brilliantly clear. We therefore continued making preparations until we had information on nearly all of the species and hybrids in *Paeonia*.

One of my other impressions of the VI International Congress of Genetics at Ithaca was a talk by Sewall Wright on the mathematics of population genetics.[2] Although I could not understand all of this work, I did realize that he was proposing some radical deviations from Darwinian natural selection. Under particular conditions, mutations, which in large populations require the pressure of natural selection to become established throughout the population, can become established by chance alone in small populations when not swamped out by alternatives having a higher selective value. This idea became firmly fixed in my mind and affected my later work.

The strongest additional impression was the general lecture given by the president of the Congress, Thomas Hunt Morgan.[3] He said that genetics will really come of age only when we know what a gene is structurally like and how it can split to give rise to two identical daughter genes. It took some twenty years to understand how that replication happened, and that took place through the work of James Watson and Francis Crick, who articulated the structure of deoxyribose nucleic acid, or DNA, in 1953.

One of the most fascinating spin-offs of my association with Saunders came when he showed me a runty little plant about two feet high bearing brownish flowers barely two inches in diameter. He said, "This plant came from British Columbia. It belongs to the only American species of the genus, *Paeonia brownii*. You might as well look at its chromosomes and see if they are different from those of the beautiful species that we have been studying."

I made the desired fixation and took it back to my lab at Colgate. On the next available weekend evening, I squashed out its chromosomes and received the jolt of my life. At the critical stage of meiosis, the chromosomes were arranged not into five pairs that we had seen in all of the other species, but were paired end to end in a ring of 10. This situation was like the well-known evening primrose (*Oenothera*) and two or three other genera, but its discovery in a genus of which all other species had the usual pairing was something new. I immediately rushed to the phone to tell Saunders about it. I found that he was out for dinner but nevertheless, gave the information to his butler as carefully as I could. "Please tell Professor Saunders that Dr. Stebbins would like to see more material of *Paeonia brownii*," I said, spelling out the word *brownii* carefully.

A few days later, Peggy and I were asked to dinner at the Saunders home, and while waiting in the entrance hall for them to appear, I happened to glance into a bowl in

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2. Wright presented the outline of his shifting-balance theory of evolution at this time. — VBS

3. Thomas Hunt Morgan (1866–1945), whose pioneering studies using *Drosophila melanogaster* fueled classical genetics, received the Nobel Prize for this work the following year. His address as president of the Congress was published under the title "The Rise of Genetics." See page 87–103 of the *Proceedings of the VI International Congress of Genetics* edited by Donald F. Jones. — VBS

which notes had been placed. One of them read, "Dr. Stebbins would like to see more of Browneyes." I quickly put the note into my pocket before Peggy saw it.

After getting squash preparations of nearly all the species and hybrids in the Saunders collection, we realized that we had three different patterns of meiosis in the collection as a whole. Most of the *Paeonia* species were diploids, in which at meiosis the 10 chromosomes form five pairs. A few of the species were tetraploid, having 20 chromosomes. At meiosis, these formed a varying number of pairs and of configurations that included four chromosomes or quadravalents. Most of the tetraploids having 20 chromosomes could be classified definitely as *Paeonia officinalis*, although when Saunders received them, they bore various other names. We decided that all but a few tetraploids, particularly those native to central Europe and the Mediterranean region, belonged to *P. officinalis*. I then started to wonder what is the origin of this tetraploid species? Looking carefully at leaves, flowers, and the nature of hairiness, I could see in all of these plants some characteristics found among the diploids only in the group belonging to *P. corallina* and confined to the Mediterranean region. Other characteristics, which among the diploids were confined to those found in Asia, including northwestern Siberia, were named *P. anomala*. Is it possible that the different tetraploids that other botanists have given various names but that to us could be recognized as varieties of *P. officinalis*, could be derived by chromosome doubling and subsequent segregation of both chromosomes and genes from ancient hybrids between *P. anomala* and peonies of the *corallina* affinity? At that time, plant cytogeneticists were familiar with a few examples of such doubled hybrids that are alloploids, and in 1930 at the International Botanical Congress in Cambridge, Edgar Anderson had called my attention to one of them in northeastern North America, so that adding another to the list was nothing remarkable. However, there were two difficulties; one of them was the great variability between the different tetraploids, while the other is the fact that at present, *P. anomala* is separated from all of the *P. corallina* types by more than 1,000 miles, or the distance between northwestern Siberia and the Black Sea. This barrier is not fatal to the hypothesis, as the migration of plants hundreds of miles southward during the Pleistocene epoch was an accepted hypothesis. This whole line of reasoning depends on finding as many examples as possible that can be explained in a similar way. During most of my career, I have looked for such examples.

In the autumn of 1934, I had received from Professor Ernest Babcock of the University of California at Berkeley an invitation to spend four years doing research financed by a grant from the Rockefeller Foundation to explore the relationships of the genus *Crepis*, a relative of the dandelion that is remarkable for the large number of different chromosome numbers that its species possess. Babcock and his students, along with the Russian cytologist Mikhail Navashin, had made hybrids and had studied both species and hybrids in depth. From their results, Babcock had proposed several hypotheses about the origin of *Crepis*, which it would be my job to test. To say that this was a tremendous boon and boost for me would be putting it mildly, and I have been always indebted to Dr. S. F. Blake, who proposed my name to Babcock.

During the entire spring of 1935, Peggy and I had great expectations and prepared ourselves in various ways for the trip across the continent. It was under these conditions that I made my farewell visit to Percy Saunders, which included a visit to his garden to fix cytological material for later use in Berkeley. When I went to his home in mid-morning of that final Sunday, the butler replied, "I am afraid that Dr. Saunders is busy. He has a very old and important friend with him."

"I wonder if I couldn't meet this friend?" I replied.

"Perhaps," he answered, "but they're not quite dressed … ."

Then in walked Percy himself saying, "Ledyard, I want you to meet Alex Woollcott." I made a surreptitious gasp. Surely meeting one of the great contemporary literary lights

in negligee costume is an experience far from the usual. I sat down and we all shared breakfast coffee.

During our informal conversation, Mr. Woollcott tantalized me with a question that I expect he had asked many times upon meeting somebody whose intelligence he expected to enjoy. "You know that every newspaper throughout the world has prepared written statements about all of the most important people in the world so that when any one of them dies, an obituary can be put into the next issue of their paper," he said. "Can you tell me your opinion of which 10 people now living would have the largest total number of lines in all of the newspapers of the world today?" I was bowled over by this challenge, but tried to do my best for the great man. I mentioned Roosevelt, Mussolini, Hitler, followed lamely with Gandhi, and then my steam seemed to run out. In 1935, Churchill was not yet on the scene and other English politicians were not that great. I realize now that another name, Charlie Chaplin, might have headed the list because of the enormous popularity of his films throughout the world. Finally, Woollcott interrupted me. "That's enough," he said. "Other people also have difficulty with this question." I realized that he had hit upon a question that, if posed at any intellectual gathering, would give rise to endless arguments. Surely, the reputation of this man as a stimulator of mental and intellectual activity could not be denied. When many years later I saw the play and the movie, *The Man Who Came to Dinner*, and was told that this was intended as a character sketch of Alexander Woollcott, I thought back to this incident and, among other things, was greatly indebted to Percy Saunders for making it possible.[4]

4. Saunders named a hybrid herbaceous peony after Alexander Woollcott in 1941, *Paeonia* ×*lactiflora* (*P. lactiflora* Pall. × *P. peregrina* Mill.) 'Alexander Woollcott.' — EPD

Chapter 12
Transplanting the Family to California

During the last week of June 1935, Peggy and I with our children, Edy, age 3, Bob, age 2, and George in utero, arrived at the Berkeley railroad station and were met by my former fellow graduate student at Harvard and companion on the European trip of 1930, Rimo Bacigalupi. He was, at that time, employed by the USDA Forest Service in an aborted attempt to make vegetation maps of California. He took us to an apartment near the campus where we stayed for a few nights before moving into a house that we had rented in north Berkeley. Shortly afterward, Professor Ernest Babcock visited me there, took me to the campus, and explained his objectives and my job. I was to investigate chromosomes of various genera related to *Crepis*, such as *Prenanthes*, *Lactuca*, and various small Asiatic genera of which the relationships were problematic. For most of these, he had acquired seed that was in the charge of his technician, Ernest Jund, and from which plants would be grown in the greenhouse and the root tips for counting chromosomes harvested when they were in full growth. He then introduced me to the rest of the department.

Ernest Babcock himself had joined the university community at Los Angeles in the institution originally called The Southern Branch, but later and up to the present known as University of California, Los Angeles, or UCLA. With his associates there he had bred a peach variety known as the Babcock peach, which was a very popular variety, although in recent years it has been superseded by others having a better flavor and texture. In about 1900, the Dean of Agriculture, Ernest Hilgard, decided to establish a Department of Genetics and Plant Breeding, and he appointed Babcock as its chairman. After his appointment, Babcock became more interested in evolution than in plant breeding and hoped to do research on and popularize a small plant known as *Crepis capillaris*, a little annual weed, because of its small number of chromosomes, only six in somatic cells and three pairs at meiosis. After a few years of research on this species, his hope that it would become a plant counterpart of the fruitfly *Drosophila*, on which T. H. Morgan and his group had made such brilliant discoveries, was dashed for various reasons. Babcock's associate, H. M. Hall, who died before I came to Berkeley, suggested to Babcock that the presence of a large number of species of *Crepis* having low chromosome numbers might provide an avenue for studying evolution of differences in whole chromosomes rather than genes. This caused Babcock to direct the research of his students toward counting the chromosomes of as many species as possible and comparing chromosome structures by making hybrids between species. When I arrived in Berkeley, this research had proceeded so far that Babcock was ready to begin preparation of a monograph of species based largely on cytological characteristics, which I was expected to amplify by comparing chromosomes of *Crepis* with those of related species belonging to other genera.

However, when I studied Babcock's publications as well as unpublished data on a small group of species native to North America, I realized that he did not really understand these species because they included problems similar to those that I had studied in *Antennaria* and *Paeonia*. I felt that I could make a contribution to the *Crepis* research itself as well as on species of related genera. When I went to Babcock to explain this situation, he warmed up immediately and suggested that I embark on both projects simultaneously. This was confirmation of my hope that I would have in Babcock a boss

who would be both highly compatible and permissive and that our collaboration would therefore give a real boost to both of us.

After I had learned all this history from Professor Babcock, I realized that I had reached an ideal laboratory for developing both his and my own concepts of evolution. When I found out later that my invitation from Professor Babcock to join him had been suggested by the friend I had made in Washington, Sidney F. Blake, I realized how important it was to become friends with as many others as possible of scientists interested in chromosomes, systematics, and evolution.

Chapter 13
The Berkeley Genetics Department

Ernest Babcock felt that the Genetics Department was of focal importance in agricultural research. He based this position on the insight of Ernest Hilgard, who was convinced that genetics would share with plant nutrition, photosynthesis, and pathology the opportunities of learning more about evolution and application of plant science to practical problems. After Babcock had become chairman, he had appointed as his second in command Roy Clausen, who had received his Ph.D. in the Department of Botany on the Berkeley campus under the direction of T. H. Goodspeed. Goodspeed and Clausen were the authors of the textbook *Genetics in Relation to Agriculture*, which arose from their research, the first demonstration that doubling the chromosome number of a species hybrid can lead to the origin of a new species, fertile within itself, and forming sterile hybrids with all pre-existing species.[1]

By the time I arrived in Berkeley, Babcock and Clausen's textbook was being used by graduate students in agricultural universities throughout the nation. Clausen had subsequently decided to continue with the genus *Nicotiana* and to analyze cultivated tobacco by obtaining a series of different genotypes, each of which had one less than the usual number for the species, 48 in somatic cells. By this method, he hoped to discover the genetic content of each of the 24 pairs of chromosomes found in the tobacco species. In addition, Clausen, along with other Goodspeed students and several foreign geneticists, chiefly Russians, believed that the tobacco species itself had originated from a hybrid between two other species, each of them having 24 chromosomes in somatic cells and 12 pairs at meiosis. These hybrids were originally completely sterile, but had become fertile by means of chromosome doubling or allopolyploidy. While I was at Berkeley, Clausen's student, Walter Greenleaf, made a hybrid between *Nicotiana silvestris* and *N. tomentosiformis*, then changed it from a sterile to a fertile genotype by doubling the chromosome number, and so produced a replica of the cultivated tobacco species. All of this research was highly relevant to the problems that I studied in *Paeonia*.

In addition to Babcock, who was 51 years old and the department's senior member, and Clausen, who was in his 30s, there were three younger members of the department about my age. Don Cameron had done his Ph.D. thesis on *Crepis* with Babcock and then became postdoctoral assistant to Clausen. James Jenkins, another former student of Babcock's, was his assistant in University-funded research, with whom I was expected to collaborate. The third young member, Everett Dempster, was still a graduate student but was doing a Ph.D. thesis on an unrelated problem, the effect of neutron radiations on mutations in the fruitfly *Drosophila*.

The members of the Genetics Department were only some of the highly capable and deeply interested evolutionary geneticists with whom I had the privilege of associating and discussing problems during my years at Berkeley. Most prominent and continuous was an informal group known as "Geneticists Associated." It consisted of Cameron, Jenkins, Dempster, and Michael Lerner, who was doing his Ph.D. research on

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1. Ernest Brown Babcock and Roy Elwood Clausen, *Genetics in Relation to Agriculture* (New York: McGraw-Hill, 1918). — VBS

inbreeding and development in chickens, as well as a succession of doctoral students whose major professors were at UC–Davis, but who were required to spend one or more years in Berkeley because at that time all doctoral students from both campuses were administered in Berkeley.[2] We met every month at the home of one of us, after having read assigned papers that had just been published and were of interest to all of us. The discussions were "free for all" as we were all essentially equal in status, and all sorts of ideas came to the surface. Later on, new faculty members in the College of Letters and Science joined us.

These young people of the Geneticists Associated discussion group, along with the graduate students that I acquired, were my principal associates both on and off campus during my final years in Berkeley. During my Colgate years, which were also the first years of the Great Depression, I had become a great admirer of President Franklin D. Roosevelt. This continued into my early years in California, where I was less worried about expressing my ideas than I was under the constrained atmosphere of Colgate. When World War II came, my draft status was 4F, governed by the presence of my three small children and by the desires of Babcock's superior, Vice President Claude B. Hutchison, to keep as many as possible of his staff and faculty at work on the home front rather than overseas.

In Berkeley, I became a loyal Democrat in spite of my mother's complaint that I had become a traitor to my class. In my mind, the whole concept of upper class had been replaced by a desire to be in tune with all people, regardless of background, who wanted to support the rights of others regardless of race or social position. I therefore strongly supported Roosevelt's campaign of 1936 and rejoiced in the Democratic sweep that we produced. During the war, the political demographics of Berkeley and other East Bay cities was radically transformed by the arrival of workers in the shipbuilding effort and other defense work.

After the war, I shifted my allegiance to Harry S. Truman. Following the direction of his former leader, he had come to the decision to drop the atomic bombs on Japan. At that time, I was also in favor of dropping the atomic bombs because I, like so many others, was weary of the war and its great costs. Later, during the Korean War, when Truman ran afoul of General Douglas MacArthur's desire to plunge us into a war with China, I felt vindicated in that earlier choice. I realized that Truman's own position was strongly for peace. During the intervening years, when Truman was running against Thomas E. Dewey for the presidency in 1948, I rang doorbells in Berkeley for him and for a liberal congressman in our district. I invited my companions, who were also helping the Truman campaign, to what we thought would be a bittersweet election with Truman losing and the man in our district winning. I was quite taken aback to come home from the campus on that fateful Tuesday evening and learn that Truman had already won Kansas. As the evening progressed, the bittersweet result became sweet-bitter as Truman continued to win and our congressman went down to defeat. This was my last extracurricular activity in Berkeley because of my move to Davis two years later.

The second discussion group of equal or broader interest that has persisted to the present day was organized by David Keck, an associate of Jens Clausen at the Carnegie

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2. In his oral history memoirs, Stebbins also referred to this loose organization as a journal club he called "Genetics Associated." It included a number of junior geneticists at Berkeley who frequently collaborated with each other: Donald Cameron, James A. Jenkins, Everett L. Dempster, and Israel Michael Lerner. — VBS

Department of Plant Biology at nearby Stanford University.[3] He called this new group "Biosystematists" and stated its objective, which was to compare variation patterns in the most diverse kinds of organisms possible and to report on research, especially that of each particular speaker, that enriches the analysis of these patterns. He invited a large number of mature scientists from Stanford, Berkeley, and the California Academy of Sciences in San Francisco. The membership of the group has changed greatly over the years. Among those active during the first few years of the organization were Alden Miller, an ornithologist; Seth Benson, an expert in native mammals; Sol Light, a specialist in invertebrate biology; Gordon Ferris, an authority on parasitic scale insects; Robert Usinger, an authority on those insects commonly known as true bugs in the order Hemiptera; Ira Wiggins of Stanford, an authority on the flora of Baja California; Reuben Stirton, a paleontologist interested principally in primates; Babcock; and myself. There is little doubt that the ideas brought forth in meetings of the "Biosystematists" were very important in the formulation of my ideas.

Finally, my horizon was greatly broadened by Babcock's decision to ask the administration to establish a course on the principles of evolution for me to teach after I had spent four years as a research worker under his Rockefeller Grant and had been appointed Assistant Professor of Genetics.[4] I put a lot of work into preparing this course, which paid off to such an extent that I was placed on the oral examination committee of graduate students in Genetics, Botany, Zoology, and Entomology. In this way I became exposed to the first ideas and accomplishments of several biologists who later became nationally known, such as Frank Pitelka and Dan Janzen. I also came to realize that the skepticism about the validity of Darwin's theory of natural selection that was widespread at Harvard and presented to me by Professor Parker in his lectures did not exist in California. Most situations either were governed by a desire to present new examples of Darwinian natural selection or were at least discussed favorably by the candidates and their major professors.

Two examples of this expansion of viewpoint are relevant. Dr. Usinger told us that the common human bedbug *Cimex lectularius* was acquired by primitive humans as a transfer from bats, as all of its relatives are parasites of bats rather than humans, and bats have been associated with humans and their ancestors in the same cave for tens of thousands of years. Another was the brilliant demonstration by the experiments of Dan Janzen that the ants inhabiting the huge hollow spines borne by species of *Acacia* known as bullhorns are vital to the plants' life. Within each of these hollow horns is a small colony of ants ready to dart out and devour any damaging beetle that may land on the plant. If, in an artificial experiment, bullhorn acacias are raised in an environment from which ants are excluded, they quickly acquire predatory beetles that kill the plant before it can reach maturity.

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3. Stebbins' recollection of the origins of the group known as the "Biosystematists" is inaccurate. The group originated sometime in 1936, largely through the efforts of a group of interested coworkers in the Bay area. It took the name of "Biosystematists" later in the early 1940s. For a history of the group see William Z. Lidicker Jr., "An Essay on the History of the Biosystematists of the San Francisco Bay Area," in *Cultures and Institutions of Natural History and Philosophy of Science: Essays in the History and Philosophy of Science*, Michael T. Ghiselin and Alan E. Leviton, eds., California Academy of Sciences Memoir 25 (2000): 315–327. For a photograph of the group in 1944 see Vassiliki Betty Smocovitis, "G. Ledyard Stebbins, Jr. and the Evolutionary Synthesis (1924–1950)," *Amer. J. Bot.* 84 (1997): 1625–1637. — VBS

4. Stebbins took over the course with Babcock's recommendation when a vacancy took place in the late 1930s. The course on evolution was taught out of the Genetics Department. He was appointed Assistant Professor in 1939. — VBS

Chapter 14
Asteraceae Research with Ernest Babcock

In this atmosphere of dedicated and progressive thinkers, I began my research with Ernest Babcock on the American species of *Crepis*. From the previous investigations of his group, we knew that genotypes placed in the same species and that could not be separated clearly from each other could have either 22, 33, 44, or 55 chromosomes. We also knew that some of the genotypes with higher chromosome numbers, particularly 33 and 44 in somatic cells, produce little or no viable pollen but nevertheless develop abundant seed. As in the genus *Antennaria*, this development could only be possible if it were parthenogenetic, that is without pollination.

Our first task was to separate diploid sexual genotypes from polyploids that might be parthenogenetic. Fortunately, I found that all of the genotypes that we had counted and found to be diploid had relatively small stomata in their leaves and had pollen grains that are regular, similar in size, and always with three pores. Those counted as polyploid have larger stomata and pollen grains that are greatly different in size even in the same flower and may have four pores per grain rather than three. Consequently, I studied dozens of dried specimens and could be fairly sure which ones were diploid with $2n = 22$ and which were polyploid having higher numbers. When all specimens had been investigated, a clear pattern emerged. The diploids were easily placed into one of five clusters. One of these was widespread but all of the others were narrowly restricted in geographic distribution. Furthermore, each diploid possessed a group of characters that was extreme with respect to the group as a whole, while the polyploids contained intermediate characters and recombination of characters that would be expected if they were of hybrid origin. The correspondence to the type of pattern that I had postulated for *Paeonia* was almost unbelievable. The whole story was reinforced by examination of ovule and seed development. The postulated diploids turned out to have the normal development of megaspores, embryo sacs, and embryos similar to that found in all normally sexual genotypes. On the other hand, the polyploids were highly irregular. Tetrads of megaspores were usually formed, but rarely if ever developed embryo sacs or egg cells. Instead, embryo sacs were produced by groups of cells from the outer cell layers of the developing ovule, which pushed their way into and replaced the expected sexual embryo sac.

This phenomenon, known as apospory, had been carefully described in several species belonging to the related *Hieracium* or hawkweed, also in the Asteraceae, which also produced seeds without fertilization. The annoying behavior of hawkweeds became known to Mendel in the 1860s after he had done his research on garden peas. His failure to account for this unexpected phenomenon was one reason he abandoned his genetic research. When the entire pattern of distribution of these North American species of *Crepis* had been worked out, the distribution of diploids was found to be chiefly in northwestern California while the polyploids were much more widespread and were the only genotypes present in those parts of the Sierra Nevada covered by ice during the Pleistocene glaciation. They also were absent from the northern rim of distribution of the group as a whole, which was northern Washington state and southern British Columbia, both of which were either glaciated or strongly affected by nearby glaciation events. We could therefore postulate safely that the differentiation of the diploids from each other took place before the beginning of glaciation, and that polyploid evolution took advantage of new areas exposed by the retreat of the ice.

Another highly interesting feature of these American species was that they were divided into two groups. One group that occurred all the way from the eastern Rockies to the western edge of the Great Basin consisted entirely of diploids and could be regarded as a single variable species. This group was confined to streambanks or the edges of moist alkali sinks so that it most probably had continued to form a more or less continuous series of populations throughout the Pleistocene epoch. The other species group, which formed the polyploid pillar complex, consisted of populations that usually grew on mountainsides or mountain valleys and inhabited a great variety of different ecological niches. Apparently their development, including hybridization, polyploidy, and apomixis, was greatly affected by hybridization between descendants of original diploids followed by adaptation by natural selection to the ecological changes during the Pleistocene epoch. The contrast between the ecological and reproductive behavior of these two groups of clearly related species was strong evidence for the hypothesis that hybridization, polyploidy, and apomixis are greatly promoted by ecological disturbance.

The rest of my research with Ernest Babcock dealt almost entirely with the relationships and possible origin of the genus as a whole. Following an initial lead from Babcock himself, I focused my attention on several genera of the Asteraceae tribe, Lactuceae, that on the basis of both growth habit and the nature of the floral heads or capitula resembled each other to varying degrees and, at the same time, showed resemblances to the well-known larger genera of the tribe such as *Lactuca*, *Prenanthes*, and *Hieracium*. My comparisons convinced me that their previous arrangement into genera was misleading, particularly because among the different accounts of the flora of the mountains of central and eastern Asia, many differences existed between contemporary publications. To me the best solution was to expand one of the genera endemic to the Sino-Himalayan region by including lesser-known species, then placed in various other genera. One group consisted of cushion-like plants found only above timberlines, mostly at altitudes of 14,000 to 16,000 feet above sea level, that were so distinctive that I regarded them as belonging to a previously unrecognized genus that I described. This research was the most extensive venture of my career into traditional, old-fashioned taxonomy, but in view of the fact that the species concerned occur in remote areas and some are difficult to raise in the garden or greenhouse, this treatment was the only possible avenue of approach toward the origin of *Crepis*. It was the conclusion of Babcock that *Crepis* arose in the mountains of central Asia. Later on, as climates became colder and wetter in the north, it migrated to the Mediterranean region and proliferated into species that could colonize new habitats produced by a general warming trend accompanied by extensive mountain building.

Chapter 15
A Switch to Research on Native Plants of California

Both my teaching and research were greatly changed in 1939 when, through the help of Ernest Babcock, I was appointed Assistant Professor of Genetics and praised by further promotions until I became full professor in 1948. Having received the objectives that Babcock set for me, I decided from then on to do research on topics of my own choosing and with reference to my position in the University of California. This meant that the groups with which I would work would be either native to California or introductions that would improve the uncultivated grasslands of our state.

I therefore chose to do research on the cytogenetics of the plant family Poaceae, the grass family, which is of the highest practical importance. My objective was to use the recently acquired knowledge of the origin of new species both in nature and in the garden to create perennial species or subspecies that would provide feed for livestock in the early fall and late spring, when the annual species that dominated dry pastures were either too small to be useful or had become mature, set seed, and become dormant.

I had in mind the perennial brome grasses (genus *Bromus*), perennial wheat grasses (*Elymus* [wild rye] and its relatives), and needle grasses (*Stipa*). The latter I quickly abandoned after learning that their seedlings are very small so that many years would be required to produce a worthwhile stand. I next tried the perennial brome grasses and immediately found that they are a very promising genus for studying processes of evolution. In particular, the three perennial species growing spontaneously in the Berkeley area, one of them native (*Bromus carinatus*) and two introduced from South America (*B. catharticus* and *B. stamineus*), possessed an array of chromosomes with a highly revealing geographic distribution. The South American species both have 42 chromosomes, forming 21 pairs at meiosis, while the North American *B. carinatus* has 56 chromosomes that at meiosis form 28 pairs, seven of these relatively large and 21 medium-sized pairs. Crosses between different South American species have 21 pairs, as do their parents, but nevertheless are sterile because neither mature pollen grains or seed are formed. The same is true of hybrids between the North American *B. carinatus*, which are either classified as *B. carinatus* or as some other species, and several other races or species. In this group having 56 chromosomes in somatic cells, known as octoploids, some hybrids between races having different geographic distributions are fertile and others are highly sterile. Differences between such entities show poor correlation between geographic distribution, differences in external morphology, and sterility versus fertility of hybrids between them, so that the classical reproductive isolation species concept cannot be applied to them.

The most dramatic results of hybridization between perennial species or races of *Bromus* occur when those from South America are crossed with highly similar North American entities. The hybrids are always sterile and in meiosis form 21 pairs of medium-sized chromosomes and seven unpaired chromosomes of larger size. The suspicion that these larger chromosomes belong to a different subgenus of *Bromus* has been verified in one example. In it, a cross between *B. carinatus*, with 56 chromosomes and *B. laevipes*, with 14 large chromosomes, possessed seven large pairs and 21 medium-sized single chromatids. This indicates that *B. carinatus*, in the broader sense, is an allopolyploid containing 42 chromosomes similar to those of the South American species and 14 chromosomes similar to those of *B. laevipes* and about half a dozen North American diploids having 14 large chromosomes.

How and when the hybridization that gave rise to these octoploids could have taken place is somewhat of a mystery. It is best explained by assuming that during the Tertiary period, species similar to the modern South American species existed also in North America. That this is reasonably probable is evident from the fact that paleobotanists have discovered a large number of fossil seeds belonging to species now absent from western North America, but present in South America. Unfortunately none of them belong to the genus *Bromus*, but to other genera such as *Piptochaetium* and *Nassella*, that have much harder seed coats than does *Bromus*.

Further investigations of *Bromus* have uncovered a number of problems connected with geographic distribution and phylogeny of species and genera. However, field tests of progeny from the hybrids mentioned above showed no evidence of increasing resistance to drought in any of the segregates that were tried. Apparently, there does not exist in *Bromus* a large store of genic material that would promote increasing drought resistance, so this genus was abandoned relatively early in the project.

I next devoted my attention to native perennial genera of the wheat subtribe Triticinae as they include a larger array of drought- and cold-resistant races, particularly in the blue wild rye *Elymus glaucus* and the rhizomatous or sub-rhizomatous *E. triticoides* and *E. condensatus*. The latter two species have so much seed sterility and such poor vigor of seedlings that they did not warrant further investigation.

On the other hand, the complex of races placed in *Elymus glaucus* and its close relatives produced abundant seed and reasonably vigorous seedlings. But when I started a carefully planned program of hybridization, I received an almost fatal blow. Many of the races, even though they were placed by all taxonomists in the same species, either could not be crossed with each other or produced highly sterile hybrids. This meant that if these self-compatible bunchgrasses were to be used at all, I would have to make a large number of hybrids, and by the use of the drug colchicine, I produced allopolyploids from them. I decided that if this was the only avenue to success, I would need to cross *E. glaucus* with species belonging to the entity then classified as *Sitanion* and create new allopolyploid species of supposedly intergeneric origin. I then made the necessary hybrids and found that in them the chromosomes derived from the parental species paired very well with each other, a situation that was unexpected in an intergeneric cross, but nevertheless the hybrids were completely sterile. When the chromosome numbers of the F_1 hybrids were doubled to produce the desired allopolyploids in these, latter chromosome behavior was more irregular than in the undoubled hybrids and the first generation after doubling had increased irregularity and much greater sterility.

These results were quite contrary to those that had been obtained by other investigators working with different genera, such as the cross between wheat and rye. My aim was to produce long-lived perennials, and the prospect of getting significant results in relatively few years was very low, even assuming that a few more fertile plants could be obtained in later generations. The species and hybrids available did not provide easy avenues toward realizing this aim. Seeds harvested from these allopolyploids and planted under field conditions performed relatively well but not well enough so that I could expect success in a reasonable number of years. No doubt genetic analysis to find out the causes of this unexpected behavior might eventually lead to new theories about the cytogenetic evolution of these plants. But this was by no means certain. What was certain was that with respect to the desired goal of creating a series of drought-resistant and agronomically valuable perennial bunchgrasses, the uncertainties as well as the long time that would certainly be necessary told me that I should look for another group of grasses that lacked these roadblocks.

I made preliminary trials of a few other native groups as well as introductions from Australia of bunchgrass perennials, but none of them was any more promising

than the groups I had already tried. I therefore turned my attention to drought-resistant perennials native to Europe and the Middle East and found them in the genus *Dactylis*, to which orchardgrass belongs. I had recently received seeds of *Dactylis* from Portugal, Israel, and Iran that included both diploids and tetraploids, all of which produced abundant seed and vigorous seedlings. Two groups of races were well-known members of the European flora bearing the taxonomic names *D. aschersoniana*, which was applied to diploid forest-loving races, and *D. glomerata*, the common orchard tetraploid grass of fields and open woodlands. Races from most parts of the Mediterranean region are tetraploid and occupy a great variety of habitats. They are fully interfertile with *D. glomerata* and form numerous naturally occurring intergradations. At first, I had only four diploids: the *D. aschersoniana* already mentioned, *D. woronowii* collected by American agronomists in northern Iran and described by Russian botanists from Soviet regions immediately north of Iran, plus a diploid from Israel and another from Portugal. A number of other races represented only by dried specimens had small stomata and pollen grains that suggested a diploid chromosome number. Furthermore, still other races that appeared to be tetraploid were sent to me from the Negev Desert of southern Israel, where the annual precipitation was only 150 to 200 millimeters.

All of these preliminary signs suggested strongly that the genus *Dactylis* would prove to be more promising than any native Californian genera. I therefore applied for and received a Guggenheim Fellowship to make a trip to the Mediterranean region.

I decided to make my headquarters at the French University of Algiers because I had had correspondence with its chairman of botany, Marcel Guinochet. He, with his staff, was investigating the ecology of the Algerian flora.

This trip occurred in 1954 and was followed by a trip to Spain and the Canary Islands where I was on my own, and to Morocco on an excursion organized by the officers of the Eighth International Botanical Congress as a preliminary to the Congress itself held in Paris in the summer of 1954.

Chapter 16
Adventures with Carl Epling and Edgar Anderson

From this point in my career, the research I pursued was either completely on my own initiative, such as that on grasses, or stimulated by the scientists with whom I became associated during the 1940s and continued as long as we could work together. The three men who helped me the most were Carl Epling, Edgar Anderson, and Theodosius Dobzhansky.

My association with Carl Epling began in 1941, when he asked me to visit with him an area near Palmdale that had an unusual pattern of variation in flower color within a small annual species, *Linanthus parryae* in the Polemoniaceae. I drove to his home west of the UCLA campus and we went in his car to the desert area east of Palmdale and Lancaster. He first showed me a map of the area that he and his graduate students had studied. The species covered most of the flat plain north of the San Gabriel Mountains. In most of this area only plants with white flowers were found, but in a few areas most of the flowers were blue. While studying the problem for several years, Epling had determined that the difference between blue and white was governed by a single gene pair. It was very difficult to explain this pattern on the basis of natural selection. He had shown his data to both Theodosius Dobzhansky and Sewall Wright, who agreed that this was one of the best-known examples demonstrating the role that chance (or random genetic drift) could play in the establishment of small populations. I had to agree with all of these data and have used this example in my own writings.

The problem was still not fully solved. Critical to the solution of this problem was a better understanding of the occurrence of blue- and white-flowered plants in regions both west and east of the area studied by Epling's group. According to amateur botanist Clare Hardham, blue-flowered plants predominated on low hills west of Lancaster. I had also seen herbarium specimens of blue-flowered plants to the east of Epling's area where again they were found on hilly ground. Even farther to the northeast in the foothills of the southernmost Sierra Nevada, a few collections had been made that appeared to contain some blue-flowered plants. I suspect that originally *Linanthus parryae* consisted of both blue-flowered and white-flowered plants to the west and east of the mapped area and that usually white-flowered plants predominated on flat plains and blue-flowered plants on surrounding hills, as Ms. Hardham had observed. If this hypothesis is correct, the chance distribution in the area east of Lancaster is a secondary phenomenon of migrations during most intervals in the Pleistocene, but the original occurrence of blue- and white-flowered populations was the further result of natural selection by different pollinators. Clearly, this problem needed much further study and would profit greatly by an approach using molecular methods.

That day in the field gave us both a chance to realize that we had many interests in common and neither of us was afraid to voice opinions about them. Epling invited me to stay with him every time I went to Los Angeles and UCLA. Our discussions of such theoretical problems as the nature of species and the origin of the flowering plants lasted far into the night. Much of his research was performed on southern Californian members of the mint family Lamiaceae, in which he had discovered a number of hybrids between species having very different flowers. In this way he had attracted the attention of Edgar Anderson so that we had three-way discussions whenever all three of us were together. In addition, Epling had one graduate student whom I advised and

helped start his research career. This student, Harlan Lewis, later became a professor at his home institution, UCLA. Lewis led a very active group of graduate students, including Peter Raven,[1] during the 1940s and 1950s. The monograph of the annual genus *Clarkia* by Harlan Lewis and his wife, Margaret, is one of the best biosystematic monographs that has yet appeared.

Unfortunately, various family difficulties caused Carl Epling's later life to be most unhappy and it ended in his over-drinking.

The second of my close scientific companions was Edgar Anderson. I met him in 1930 at the International Botanical Congress in Cambridge, where he gave evidence indicating that the common species of the genus *Iris* found in New England resulted from hybridization between a more southerly species, *I. virginica*, and a subarctic species, *I. setosa*, found in eastern Alaska and adjacent Canada. I have since seen both species in their native habitats and can only agree with his opinion. This hypothesis, like the one I had suggested about the origin of *Bromus carinatus*, implies that the two parental species now widely separated from each other by the distance of the Great Lakes to western Canada were formerly growing side by side in the intervening area, which during the height of the last Ice Age had a suitable climate for both of them.

Edgar Anderson did a great deal to help me look at plants from the standpoint of a biologist and a naturalist. When I wrote him that I had started to do research on grasses, he immediately called my attention to research being done by one of his students on Kentucky bluegrass (*Poa pratensis*) in which the precise timing of vegetative and reproductive phases agrees with the habitat of the species that tolerates harsh winters and flowers during the summer season in luxuriant meadows. He also showed me his method of reducing complex patterns of variation within petals of flowers such as *Iris*, artificially modified patterns that enabled him to estimate accurately the amount and position of different colors and of the pairs of lines that serve as guides to pollinators. He showed me an example of this technique on a beautiful spring day when we drove together to San Bruno Ridge, south of San Francisco.

It was in 1943, I recall, a rare day in March that was sparkling as none others can be in San Francisco. The rainy season was over. The fog had not yet begun and the city and its suburbs shone in the brilliant sunlight. At that time I was Assistant Professor of Genetics at the University of California at Berkeley, and Edgar Anderson, then a researcher with the Missouri Botanical Garden, had come there on a Rockefeller grant to work with Carl Sauer of our Geography Department and was occupying a neighboring office. That day Edgar asked me to go with him and explore variation among the flowers of a rare species of *Iris* that was unknown to him and related to others on which he had made observations.

We drove from Berkeley across the San Francisco Bay Bridge, down the peninsula to San Bruno Ridge, which separates the city proper from South San Francisco. We left the state highway at the foot of the ridge, drove up a secondary street until it ended in a broad expanse of grassy hillside dotted with flowers, including the iris. This species of *Iris*, bearing the scientific name *I. longipetala*, was the particular object of our research trip and our work for the day, as it is known only from the Greater Bay Area. We got out. Edgar, with his notebook in hand, was ready for me to pick individual flowers and hand them to him so that he could make notes according to a precise code he had devised. The recording went on for about a dozen specimens.

Edgar then threw himself on the grassy sward, looked up at the sky, and said, "Ledyard, aren't we the luckiest people in the world? Here we are, in one of the most beautiful

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1. Peter Raven, Director of the Missouri Botanical Garden since 1971 and a leading advocate for conservation and diversity, received his Ph.D. in Botany from UCLA in 1960.

areas in the world one could imagine, surrounded by these flowers with their most intricate pattern of organization in their petals, recording this in a way other people can understand, and calling it work."

I agreed with him that this was the most delightful and fortunate position we could have occupied. In the vicinity of San Francisco, there are several species that are very restricted in distribution, a few of them extinct, and in addition, *Iris longipetala*, which was probably nothing more than a race of *I. missouriensis*. Edgar Anderson was one of the few people with whom I most enjoyed spending a scientific day as I did in that March of 1943. And California was my preferred botanical area, and most of my important discoveries and observations were made with respect to the flora either of California or of neighboring states.

Another typical Andersonian adventure occurred during this same visit. I like to tell this story in Anderson's words rather than my own:

"When I went to Berkeley to be with Carl Sauer, it was 1943 and the middle of World War II," Edgar said. "I soon heard that the sororities were having difficulty in finding waiters to attend to their meals, so I offered my services to one of them, which they eagerly accepted. When, the next day, I told Ledyard what I had done, all of the sober New England blood curdled in his veins and he said, 'You would do anything to be bizarre, wouldn't you?'"

Another example of Andersonian wit that could have been embarrassing occurred when the Genetics Society of America held its meeting in Dallas, Texas, on December 27, 1941. This was three weeks after Pearl Harbor. One of the most persistent speakers at these meetings was Professor George H. Shull, who regaled us every year with a complex account of genetic abnormalities in a plant known as shepherd's purse or *Capsella bursa-pastoris*, sometimes called bursa. While the whole room was trying to decipher a slide containing hundreds of words and formulae in small type, I noticed Edgar's hand holding a note for me to pick up and read. He had scribbled, "Times are bad and getting worser, but G. H. Shull still diddles with Bursa."

As soon as Shull's talk was over, I leaned back to Edgar and whispered, "You should be made poet laureate of this society." Edgar then threw his head back and uttered a loud guffaw, which coincided exactly with the end of the mild applause the audience gave Shull for his talk. Everybody turned around, and it seemed as if I must have been making an uncomplimentary remark, which I certainly wasn't. I went up to Shull shortly afterwards and without mentioning the incident, told him that I much respected his research, which was the basis later applied to produce hybrid corn, and hoped that I would see him again sometime. He seemed happy and later on, when I gave my Jesup lectures in New York, Shull came up from Princeton to listen to me.

My favorite Anderson story occurred in Berkeley in 1951, when we were both former officers of the Society for the Study of Evolution, and the paleobotanist, Ralph Chaney, was the society's vice president. He invited all of us to his home in North Berkeley for lunch. However, lunch was delayed while he gave us a guided tour of his garden, in which he had planted many species that are well known in the fossil record and therefore ancient survivors of previous geological periods. One of them, *Cercidiphyllum*, attracted me so strongly that I lagged behind in order to see better its unusual branch structure. I didn't realize that at the other end of the branch at which I was looking, there was a nest of paper wasps that soon came buzzing out after me. I stopped my examination immediately, and I doubt if anybody has made as fast a trip from the Eocene period through the Oligocene and Miocene to the present than I did. My arrival at the lunch table caused a few raised eyebrows, as I dashed up to the table out of breath, as if I hadn't had a square meal in weeks. When questioned as to my bizarre arrival, I reluctantly told them what happened. Edgar nodded his head for a brief moment then came out with this dilly: "The day was hot, our host was gracious, but Ledyard got stung in the early Cretaceous."

Chapter 17
Theodosius Dobzhansky

Nobody can deny that the leader of the storm of interest in evolutionary theory during the middle of the 20th century was Theodosius Dobzhansky. He was the only scientific evolutionist who combined a thorough knowledge of what was then modern genetics based on the research and theory exemplified by the research of Thomas Hunt Morgan and his associates with an extensive knowledge of and deep interest in the forces of evolution that operate in nature. Dobzhansky also was enormously persuasive; like all examples of messianic promotion of a cause, his enthusiasm was contagious. Furthermore, he had planned a campaign that would supplement his own writing with that of specialists in related fields, such as George Gaylord Simpson, Ernst Mayr, and myself, to produce a well-balanced synthesis of contemporary theories. I first met Dobzhansky in T. H. Morgan's laboratory at the California Institute of Technology, where he was studying the chromosomes of the vinegar fly *Drosophila*, using the prevailing techniques developed in that laboratory. His aim was to find out whether relative distances between the genes lined up in order on a particular chromosome were similar to or different from each other when estimated on the basis of genetic recombination by crossing over as compared to estimates based on measuring the chromosomes themselves on the basis of translocations. This technique soon became outdated when direct measurements of chromosomes could be obtained by squashing out the giant chromosomes found in the cells of the salivary glands of *Drosophila*, a technique Dobzhansky adopted a few years later. During the late 1930s, he made several visits to the Genetics Department of the Berkeley campus of the University of California in order to discuss this and other problems of population genetics with our colleague, Michael Lerner, whom he had met under most unusual circumstances.

Lerner was basically a Russian. He was born in Harbin, Manchuria, of Russian parents and his native language was Russian. At the age of 10, his parents sent him to an English-speaking school so that he was fluent in both Russian and English. Later on, at the age of 17, he broke away from his parents and school in Harbin. On his own initiative, he worked his way to British Columbia where as a political exile he received an immigrant visa and a job at the University of British Columbia, doing menial work in the Zoology Department in the poultry science laboratory and chicken barns. There, he attracted the attention of Professor V. S. Asmundson, at that time the leading geneticist of the University of British Columbia. He was therefore recommended for a pre-doctoral scholarship at UC–Berkeley, where I met him in 1935.

While Michael Lerner was working in the poultry laboratory, he took university courses in biology, including genetics. Being almost the only person in North America who was at the same time a well-trained geneticist and bilingual in Russian and English, he was an ideal interpreter for a conversation between an English-speaking scientist who knew no Russian and a Russian-speaking scientific visitor who knew no English.

During a relatively brief but crucial period when Dobzhansky (Doby) and his wife Natasha were staying in Vancouver, Michael became a close friend of them both and helped them to become better adjusted, especially during one incident. After Doby had been with Morgan at Caltech for about four years, his student visa to the United States. had expired and he needed an immigrant visa in order to enter the country with the prospect of becoming a citizen. His chief, T. H. Morgan, asked the chairman of the

University of British Columbia Zoology Department to receive Dr. and Mrs. Dobzhansky and help them obtain an immigrant visa to the United States. The chairman responded with alacrity, received the Dobzhanskys and got Doby in touch with the only Russian he knew, Michael Lerner. During the few days that Doby could reside in Canada with a visa from the United States, Morgan made appointments for Dobzhansky with the U.S. Consul at Vancouver. Unfortunately, Doby's conversation with the U.S. Consul went badly. Almost immediately, the Consul asked Dobzhansky whether or not during his stay in the United States he had done any work for compensation. He had to admit that this was so.

"You have broken the rules of the student visa under which you entered our country," the Consul said. "Under these conditions, it is absolutely impossible for us to issue you an immigrant visa."

In complete desperation, Doby went to the Zoology chairman and related his plight. He had overstayed his leave away from the U.S.S.R., and if he should return, he would almost certainly be sent to jail or more likely a Gulag concentration camp. His visa for entrance to Canada was good for only a relatively short time, and now he found that he could not even go back to the United States.

The Zoology chairman phoned Morgan and related to him the unfortunate events of Doby's struggle. Morgan urgently telephoned the office of Dr. Robert A. Milliken, the president of his institution, Caltech. There, the administrative adviser said that she could not reach Milliken because he was in Washington.

Upon hearing this frustrating information, Morgan urgently said, "Find out where Milliken is in Washington and get him on the phone. It is imperative that I speak to him immediately."

It turned out that Milliken and his friend, President Herbert Hoover, were together on a yacht on the Potomac. Milliken immediately telephoned Morgan and got the whole story. Morgan explained that this young man was the brightest person in his laboratory and with a very bright future in the United States, if he could be admitted. Milliken then told the whole story to President Hoover, who immediately telephoned the Immigration Service in the State Department. The urgent message arrived at the consulate in Vancouver soon enough so that Doby and Natasha were granted immigration visas. Needless to say, from then on the friendship between Doby and Michael Lerner became even warmer and they took advantage of every opportunity to see each other.

My own friendship with Doby began during World War II, when he decided to study the inversions in *Drosophila pseudoobscura* and its relatives, using as his headquarters a cabin on the edge of Yosemite National Park in the Sierra Nevada. The cabin was under the disposal of Jens Clausen as part of his grant from the Carnegie Institution. About 1943, I decided that I would visit Clausen there so as to sit at the feet of the great Theodosius Dobzhansky and acquire knowledge necessary for my forthcoming lectures and probably a book. When I arrived, Doby greeted me most cordially but at the same time, I realized that nobody can absorb knowledge by sitting at his feet. When not asleep or eating his meals, Doby was either going from one neighboring tree to another to catch flies for his research or was sorting the flies, making the squash preparations necessary for extracting the salivary chromosomes, examining these preparations, or taking his recreation in his particular way. This was to mount a horse and ride as rapidly as possible in some direction. Any bits of wisdom that I could possibly absorb had to be absorbed either during meals or riding another horse in the same direction as the master. Fortunately, my experience at Cate School made me both interested in and capable of riding with him.

One momentous ride was to a high meadow about five miles away from the cabin. There I found two species of grasses on which I was working, *Elymus glaucus* and *Sitanion hystrix*, which I could easily tell apart while I was sitting on a horse. In addition the meadow contained a large number of plants that were intermediate with respect to growth

habit and could be hybrids. I therefore allowed my horse to munch at the grasses in which he had a different but avid interest, while I, without dismounting, picked a flowering head of *Elymus*, one of *Sitanion*, and a probable hybrid. After picking apart the spikelets of the flowering heads, I verified on the basis of both the floral characters and the presence of fertility of the species and probable sterility in the hybrids that the meadow in fact contained a large hybrid swarm. I then rode up to Doby, who was also resting in the saddle, and demonstrated my story to him. His eyes glowed with excitement.

"Stebbins, you have made a great discovery," he said. "You are the first person who has seen, collected, and identified a hybrid between species from the back of a horse."

Coming from one of the world's leading geneticists who, in a previous summer in his native land, had ridden more than 4,000 kilometers on horseback while investigating the ancestry of the domestic horse, this was truly a compliment.

Later on, I decided that I would kill two birds with one stone by demonstrating to Dobzhansky how great was the sterility of these hybrids and finding out myself whether they ever set seed. I therefore went back to Berkeley but returned to the cabin shortly before Doby went back to New York. At that late-season date, the *Sitanion* plants had all matured their seed and were easily recognizable to anybody, as well as being largely knocked over. The *Elymus* plants retained some seed, but were also easily recognized by the short and straight awns on their spikelets. The hybrids were easily distinguished by their shorter stature and longer awns on their spikelets. I therefore asked Doby to gather as many fruiting heads of hybrids as he could and put them in a bag that I presented to him, so that later he could sift through them to search for any seeds they might bear. I promised him a bottle of beer for every seed he could find.

At this he remarked, "You're a piker, Ledyard. When I was in Mexico with Michael White, he wanted to have females of a rare mantid insect that he was studying the chromosomes. He promised me a bottle of champagne for every mantid."

I was still of the belief that he would find so few seeds that I became magnanimous and replied grandly, "All right, it's a bottle of champagne for each seed."

At this, Doby enlisted his daughter Sophie to help him and together they filled my bag with seed heads. After we had returned to the cabin, they spread the material out and searched. They finally came up with 25 seeds after having looked at several hundred seed heads which, if as fully fertile as the parents, would yield between 50 and 100 seeds. I was dismayed but I stuck to my bargain. Fortunately Doby and Sophie agreed that they could not drink that much champagne. Nevertheless, during the fall of 1946 when I was staying with Doby and Natasha in New York, we did have a champagne party to honor the event.

This venture could not be capitalized upon immediately, because the source of the pollen that might have produced the few harvested seeds was completely uncertain. I therefore decided upon a more carefully controlled experiment, which was conducted in the garden at Berkeley. I made the cross between two known parents and grew the F_1 hybrid to such extent that I could make 30 clonal divisions of this one plant. I also divided into a similar number clones of the *Elymus* parent of this hybrid and interplanted hybrid and parental clones in such a way that a maximum amount of pollen would fall on the flowering but sterile hybrids. After I had allowed enough time to be sure that there was a optimum chance of *Elymus* pollen falling on the hybrids, I cut back the *Elymus* clones and harvested the culms and spikes of the hybrids. From this experiment, I estimated that I had harvested about 40,000 hybrid spikelets, which yielded 10 seeds. Of these, only one plant grew to maturity and it yielded hardly any fertile seeds at all, the total number of which was 30 percent fertility, assuming that every floret harvested could have yielded one seed. These few plants were allowed to self-pollinate and gave rise to offspring having a high fertility and a morphology within the range of the *Elymus* parent, from which they were now removed by two generations. When these pseudo

Elymus plants were backcrossed to progeny of the original *Elymus* parent, these third backcross hybrids were highly sterile. I had in essence reduced, in the second generation of backcrossing, a number of plants that behaved toward their *Elymus* grandparent in the same way that different races included in the taxonomic species *E. glaucus* differ from each other. The taxonomic species *E. glaucus* actually consists of a large number of intersterile races.

My interpretation of these results was supplemented by the fact that F_1 hybrids between *Elymus* and *Sitanion* demonstrated good pairing between parental chromosomes at meiosis, so that if one knew no more than these facts, one would conclude that the differences between the parents were genic and not associated with chromosomal differences. However, as mentioned earlier, somatic doubling of these sterile hybrids with the aid of colchicine caused their fertility to rise to 80 percent, very difficult to explain unless one assumes that the original differences between the parental races consisted of small structural rearrangements that cause much of the F_1 pairing to be between nonhomologous chromosomal regions. I believe, therefore, that in the *E. glaucus* complex plus *Sitanion*, differences between intersterile races are due not to unfavorable mutations but to small rearrangements involving a few nonhomologous genes. In 1997 Dr. Mary E. Barkworth, for the new Jepson Manual, renamed these *S. hystrix* as now *E. elymoides* subsp. *californicus*.[1]

Dr. Dobzhansky's visits at the Mather cabin were occasions of a succession of very informal symposia that a number of geneticists attended. The most notable of these underlined a weakness in all of the research on the more widespread species of *Drosophila*. This is the difficulty of estimating the factors of their external environment and therefore the relative importance of various selective agents in guiding evolution. In temperate regions, the flies are too scarce to be gathered, as are butterflies or ants, by sweeping nets through the air or picking animals off the ground. They must be attracted to food-bearing traps and collected from these traps. How far and from where they fly into the traps is completely unknown. The only certain way of getting clues about their ecology is to discover where their larvae feed. Since their food always consists of living yeast cells, this food source must always be hunted down.

While Dobzhansky was doing his research on California species, another geneticist, Hampton Carson, was investigating *Drosophila* species of the eastern states and discovered populations of larvae on yeast cells growing on slime exuded from the fermenting sap of oak trees. Consequently, as soon as Dr. Carson was invited to Mather, he looked at the large oak tree standing directly in front of the cabin and, on an actively exuding slime flux, noted both yeast cells and larvae of *D. pseudoobscura* feeding on them. When Doby's friends learned about this, they were eager to visit with him and Hamp to see this exciting discovery. Several pictures have been taken of geneticists carefully scrutinizing the developing young of one of the most important model organisms in genetics. The whole question of *Drosophila* evolution and ecology was the expected outcome of these visits.

One Mather symposium was interrupted abruptly by unexpected excitement. Among the visitors at this symposium were two of my favorite Ph.D. graduates, Jim Walters, then teaching at the Santa Barbara campus of our university, and his wife, Marta, who was working on chromosomes of *Bromus* at my suggestion, but had so little interest in

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1. J. G. Smith described both *Sitanion hystrix* in *USDA Div. Agrost., Bull.* 18 (1899): 15, and *Sitanion californicum* (1899): 13. M. E. Barkworth transferred *Sitanion californicum* not as a species but as a subspecies to another genus in Poaceae, as *Elymus elymoides* Swezey subsp. *californicus* (J. G. Sm.) Barkworth, *Phytologia* 83 (1998): 306. This Californian segregate as well as *Sitanion hystrix* were placed within *Elymus elymoides* (Raf.) Swezey by Barkworth in her generic treatment of *Elymus* in J. C. Hickson, ed., *The Jepson Manual, Higher Plants of California* (Berkeley: University of California Press, 1993): 1254. — VCH

Drosophila that during the session she wandered about looking at the scenery. In the middle of the session, we were interrupted by a blood-curdling shriek, after which Marta appeared with astonishing speed.

She rushed up to us and shouted, "There's a rattlesnake down there!" As the Mather area is the site of a summer camp run by the city of San Francisco as well as the Carnegie Cabins, we all realized that a rattlesnake was a most unwelcome visitor. We all ran down to where we heard the violent buzz of the snake and did our best to dispose of it. However, the most efficient ways of killing snakes, either by pistol shot or by using a long-forked stick to pin its head down, were either not available or we lacked confidence to perform the task safely. And so, the geneticists pelted the poor reptile with stones picked off the ground and thrown with such poor aim that they either missed altogether or hit some part of its anatomy that the snake could tolerate. After about 10 minutes of bombardment of the ophidian counterpart of the martyrdom of St. Stephen, a stone finally hit it directly on the head and enabled us to approach gingerly and perform the final execution with a kitchen knife. I can assure you that we were all perfectly sober and that the inefficiency of the job was due to our unfamiliarity with any wild animal larger than a *Drosophila* fly.

A more complete disaster occurred on another occasion. Dobzhansky followed an evening session with a trip to the timberline station that required a drive over the Tioga Pass road, which was at that time narrow, winding, and so clogged with traffic during the middle of the day that he had to make a very early start. Before we went to bed, he gave us careful directions on how to close the back porch of the cabin, which contained the refrigerator in which all of his food was stored, plus other food items and cutlery that were kept in drawers. He then locked up the main part of the cabin and asked us to get our own breakfast after he had left and to leave the porch in as neat a condition as possible before we left for Yosemite Valley, which several of the foreign graduate students wanted to see. We followed his instructions as carefully as possible, but I became an "absent-minded professor" with respect to our own stuff. When we got to the valley, I discovered that I had negligently left our lunches on the kitchen porch table so that I had to treat my visitors to a cafeteria lunch instead. Later, I wrote a note thanking Doby for his hospitality, expressed regret at leaving the lunches on the table and hoped that he was able to dispose of them to his own profit. He wrote back shortly and replied that he had not been able to dispose of the lunches since that had been done for him by an unwelcome visitor. Apparently the odor of the lunches attracted a bear that had no difficulty tearing the screen off the kitchen door and eating the lunches and other food. All food not in the refrigerator was scattered all over the kitchen. The table drawers had been opened or torn apart and the entire place was a shambles. This oversight of mine required a humble apology and payment for repairs and caused considerable embarrassment. Fortunately, no permanent damage had been done.

One of the notable features of visits to the Mather cabin by my graduate students and me was breakfast. Doby was very fond of french toast and particularly proud of his ability to prepare it by himself. The students therefore were surprised and enormously pleased to sit down at the breakfast table and be served french toast by one of the world's leading evolutionary geneticists acting the role of a gourmet chef.

During one of these sessions, Doby told me more about the invitation that I had received to deliver the Jesup Lectures at Columbia and explained more about his general plan of a multi-authored synthesis of evolutionary theory. He was forming this theory at the suggestion and with the help of Ernst Mayr and George Gaylord Simpson, at that time in New York, and Julian Huxley in London. He had previously invited Edgar Anderson to write the necessary book about plants, but the lectures that Andy gave in his Jesup series were not well received by the zoologists, and Andy was unwilling to write

them up in book form.[2] I promised that I would write a book, and while preparing the lectures, kept this need in mind.

2. The person responsible for organizing the Jesup Lectures (and making the formal invitation) was the mammalian geneticist and friend of Dobzhansky, L. C. Dunn at Columbia. It was at Dobzhansky's recommendation that Dunn invited Stebbins to deliver the Jesup Lectures of 1946. Ernst Mayr delivered the lectures along with Edgar Anderson. Ernst Mayr's lectures were published in 1942 under the title *Systematics and the Origin of Species. The Viewpoint of a Zoologist.* The companion volume covering the "viewpoint of the botanist" was never completed by Edgar Anderson, for reasons that remain unclear. There is some indication that Mayr and Anderson did not agree on some fundamental principles of evolution, namely the importance of phenomena such as introgressive hybridization (or introgression), which had been most clearly articulated by Edgar Anderson and known to take place in plants. Whatever the nature and extent of the disagreement between Mayr and Anderson, it is not sufficient to explain the failure to publish the companion botanical volume. For one attempt to understand Anderson's complex career and personality see Kim Kleinman, "His Own Synthesis: Corn, Edgar Anderson, and Evolutionary Theory in the 1940s," *J. Hist. Biol.* 32 (1999): 293–320. Stebbins' notes for his evolution course at Berkeley were the backbone for his Jesup Lectures of 1946. The lectures were published in 1950 under the title *Variation and Evolution in Plants.* The overall efforts by workers such as Dobzhansky, Mayr, and Simpson, along with Huxley, Stebbins, and others to integrate understanding of evolution with Mendelian genetics is referred to as the "evolutionary synthesis" or the "modern synthesis of evolution." — VBS

Chapter 18
The 1946 Jesup Lectures via the Missouri Botanical Garden

My stay in New York in the autumn of 1946 for the Jesup Lectures was preceded by a week-long visit with Edgar Anderson in St. Louis, followed by a bus and train trip to New York during which I stopped at the Universities of Illinois, Indiana, and Ohio State, where I had been asked to give lectures. The visit with Edgar was the longest continuous time in which we were both together. In addition to seeing the Missouri Botanical Garden, we made trips to the Arboretum (affiliated with Washington University and the Missouri Botanical Garden), which was 35 miles away in beautiful countryside. He showed me one of the features of this area, consisting of limestone barrens or glades in which the forests gave way to sparse stands of juniper and a series of rare species of rock plants belonging chiefly to the mustard family Brassicaceae, *Leavenworthia* and *Lesquerella*. The origin and evolution of these plants was not known, so that we had much interest in devising theories to explain it. Later on, a fine series of research studies on these glades was done at Harvard's Gray Herbarium by Reed Rollins.

Two interesting incidents about this visit come to my mind. One of them was that an artist friend of Edgar's living in St. Louis decided that scientific drawings of intestines, kidneys, and other interior animal organs had artistic value and so were worth a public exhibition, which she was preparing. Her friends suggested that she should have at least one painting that was more sober and had human interest. She had already done a portrait of Edgar Anderson working on plants at the Arboretum. She painted the portrait on a hot day when Edgar's torso was completely bare except for a hand lens microscope hung around his neck. After her exhibit closed, she found that the principal comment was that she had put together a fine show, but why did she have to include that enormous, bare torso?

The other incident occurred just before the day Edgar drove me to the University of Illinois at Urbana–Champaign. His advice about that visit was typically Andersonian, as follows:

"Do you know George Neville Jones?" When I said no, he continued, "Let me tell you about him. He got his initial botanical knowledge almost by himself in a small institution of western Washington, then wrote a very fine book on the flora of the Olympic Mountains. This attracted so much attention that he earned a scholarship at Harvard, where he worked under Elmer Merrill, one of the important systematists of his day, a fact that Merrill himself would not only fail to deny, but would build up on his own. At Harvard therefore, the countrified subordinate George Jones was so humble that he hardly ever spoke. However, after his scholarship, he was appointed as assistant professor at Illinois, where I visited him many times. Year after year, his confidence grew so that now when we meet, he greets me as one African potentate to another."

The next day we drove to Urbana and when we reached the Botany Department a tall, stately gentleman greeted us and was introduced as Professor Jones. He smiled graciously and every gesture was one of royal cordiality. Fortunately, I needed to smile and look gracious in my turn so that I could successfully suppress my remembrance of Edgar's characterization given to me the night before.

My visit to Urbana was very pleasant but botanically profitable only because of an experiment that had been conducted in the Agronomy Department on the effect

of selection for protein content in kernels of corn. The current wisdom among geneticists was that selection for a single character would yield results only after a small number of generations, after which the gene pool would have revealed its supply of genes for that character. The Illinois group had shown that this was not so by selecting for increased protein content for 50 generations and still getting results. The selective ears of corn that they showed me bore out their contention but emphasized more strongly another and more important side effect. The ears were small, had irregular rows and were generally unacceptable to corn breeders. The lesson taught by the experiment was that, given a reasonably large gene pool, one can select for a particular character for many generations. However, such selection for one character, when the changes in other characters are ignored, leads to highly unbalanced combinations and therefore may be greatly harmful for the genotype as a whole.

When I got back to Berkeley, I learned that selection for a single character had also been carried out by Michael Lerner on chickens and had likewise produced harmful abnormalities.

From Urbana, I took the bus to Bloomington, Indiana, the site of Indiana University. There I was met by Marcus Rhoades, a well-known corn geneticist who showed me his research on the dotted gene in corn (*Zea*) exploited by Barbara McClintock in the research that eventually brought her the Nobel Prize in Medicine. I also discussed with Ralph Cleland his research on ring-forming races of *Oenothera* in Onagraceae.

An incident that happened during this visit taught me one way to please a highly estimated young colleague. My final scientific visit at Bloomington was with H. J. Muller, the eminent *Drosophila* geneticist who received the Nobel Prize as the first geneticist to induce artificial mutations. Naturally, I was considerably in awe of him.

After Muller had shown me his latest experiment, he asked, "Where are you going from here?"

"To Ohio State," I replied.

"That's great," he said. "I'll have to phone Larry Snyder and tell him you're coming."

Muller rang up Columbus, got Dr. Snyder and exclaimed, "We have Stebbins here." The way he emphasized my name, almost an exclamation, made me feel that if such an important person spontaneously spoke in such a way about me, I had arrived in a position of prominence or would soon do so. In more recent years, when I have had occasion to speak to my colleagues about younger and promising scientists, I remember this incident and have tried to do for them what Muller did for me.

This visit to Columbus and Ohio State was comparatively uneventful. I traveled on to New York, was cordially greeted by Doby, and began with him one of the most fruitful collaborations of my life. He absolutely insisted that I live with him, his wife, Natasha, and his daughter, Sophie, in their apartment for my entire three-month stay in New York. My intimacy with this eminent and highly intellectual family I still regard as one of the high points of my life.

I usually spent the noon hour with Doby, various students and postdoctorals, plus John Moore, a professor of zoology at Columbia's feminine half, Barnard College, and an expert on the reproductive biology of frogs. The stimulus afforded to me was increased by visits to Columbia, the New York Botanical Garden, and the Cold Spring Harbor Biological Laboratory, whose director at that time was a friend of Doby's, Milislav Demerec, then beginning his research in microbial genetics.

The most interesting field trips in the New York area were with Columbia University botanists to the New Jersey pine barrens and a weekend in northern New Jersey with zoologist Ernst Mayr. Botanical observations were made chiefly on populations of *Quercus* or oaks. The most dramatic results came from a comparison of the same two species, black oak (*Q. velutina*) and scarlet oak (*Q. coccinea*). In both localities, the two species were side by side or at least close enough that pollination between them was

frequent as was evident from the presence of hybrids. However, in the New Jersey locality, the ecological distinctness of two habitats, poorly drained swamp and dry upland forest, was so distinct that the scarlet oak and a few hybrids similar to it were found in the swampy area while the black oak (*Q. velutina*) and hybrid derivatives similar to it grow in the upland dry forest. On the other hand, the landscape near Cold Spring Harbor had a rough topography as it was part of the Pleistocene terminal moraine. This was associated with a more or less random distribution of both parents and hybrids, because genotypes more similar to scarlet oak grow in depressions while those more similar to black oaks grow on drier hillocks. Combined with evidence already available and that which has been obtained by other research workers in more recent years, this comparison shows that the ultimate evolutionary effects of hybridization depended to a large extent on the edaphic factors to which second and later generation descendants are exposed. Oaks contribute some of the best evidence for the situations ascribed by Edgar Anderson to "hybridization of the habitat."

Immediately after the Jesup Lectures and while I was still on the East Coast, I attended a high-level symposium organized by Glenn Jepsen and others on principles of evolution. It was the first time that British evolutionists such as J. B. S. Haldane and Julian Huxley met with evolutionists from North America. At the same time, an international Society for the Study of Evolution was organized with the paleontologist G. G. Simpson as its first president. In 1950, I was elected as the third president of this society, following J. T. Patterson. Meanwhile, the society started publication of its journal, *Evolution*, which continues to be one of the world's leading journals that publishes accounts of direct observation and experiment in the field of evolution.

Chapter 19
Politics and Polyploidy at Davis

After I got home from the East Coast early in 1947, my attention was concentrated for two years on the book that I based on those lectures, *Variation and Evolution in Plants* (1950). Meanwhile, Professor Ernest Babcock received a phone call from the University's Vice President for Agriculture, Claude B. Hutchison, asking if any member of our department would be interested in going to Davis and aiding the University's effort to upgrade and broaden that campus by starting a Department of Genetics. This seemed to me to be an opportunity that I should consider carefully. On the one hand, I was already a full professor on the Berkeley campus where my course in evolution was well organized and was attracting a respectable number of upper division and graduate students from all over the campus. My position was giving me a chance to become associated with faculty members in other departments through my appointment to Ph.D. oral examination committees and occasionally appointment or promotion committees in Botany and for the Museum of Vertebrate Zoology. On the other hand, I was collaborating in research on the cytogenetics of forage grasses with Merton Love, who had recently been appointed to the Agronomy Department at Davis and was, like myself, a plant cytogeneticist. In addition, my wife Peggy had already asked for a separation, which to me meant probable divorce during the next few years, so that starting a new social life in the Davis environment seemed like an encouraging possibility. After a conference with Vice President Hutchison, who said that if I accepted his offer he would give me free rein to select and recommend an animal geneticist to form a second member of the department, I decided to make the shift. I arrived in Davis at the beginning of the spring semester 1950.

At first I rented a room in a private home adjacent to the campus. I found later that soon after my arrival, my social and political orientation became well known. First, I was asked to join the Davis Democratic Club, which in that election year was a champion of Helen Gahagan Douglas for U.S. Senator against Richard Nixon. In the following year, I bought my own house, while a graduate student of my colleague Charlie Rick took over that room, thereby finding out what the landlady thought of me.

According to him, she said, "Professor Stebbins is a very nice, polite man, but he's a terrible radical." That reflects the political climate of Davis when I arrived, a climate that changed during my stay as the campus was being built up with non-agricultural faculty members, many of whom were Democrats. The change is epitomized in a headline that the student newspaper carried on the day after the 1972 election, McGovern versus Nixon, which read, "McGovern carries Massachusetts and Davis."

Another event that occurred in my early years with the Davis Democratic Club was connected with the 1952 presidential campaign between Dwight D. Eisenhower and Adlai Stevenson. At that time, the governor of California was a Republican, Earl Warren. His remarkable political savvy and vision were brilliantly emphasized when President Truman's whistle-stop campaign in support of Stevenson entered California. Warren was campaigning for Eisenhower. Nevertheless, the governor commandeered a train that ran from Sacramento to near the Oregon border, where Warren joined Truman's visiting train. When this Stevenson campaign train reached Davis, we of the Democratic Club were there in force to welcome Truman. At the same time, we observed several young fraternity men who were also waiting for the train. Earlier in Truman's campaigning for

Stevenson, rotten tomatoes and other garbage were thrown at him by overzealous Republicans, making us apprehensive that similar insults would be committed in Davis. We were much relieved when the train stopped at the Davis station and the first person to appear at the back platform was Governor Warren. He looked at his audience and remarked, "Some of you here may be contemplating unkindness toward my co-traveler on this train. You must realize that he is the President of the United States and deserves the consideration reserved for his office." As a result, not a single one of the paper sacks carried by the students was opened. After watching this performance. I became more than ever impressed with the fairness of our governor and therefore followed with great interest his later career as Chief Justice of the United States Supreme Court and a champion of equal rights and integration.

As soon as my living arrangements were formalized, I set about looking for a companion in the department. Hutchison had specified an animal geneticist, but had told me only that I should get the best man possible, hopefully a scientist who would eventually be elected to the National Academy. The candidate whom I recommended and who became associated with me in the autumn of 1950, was Melvin Green, a *Drosophila* geneticist from the background of the T. H. Morgan school and its transplants at the universities of Minnesota and Texas. In his research, Mel Green filled the requirement excellently, since he was elected to the Academy during the 1970s. As a co-teacher, however, he created problems. He was very bright and, up to his retirement, was fully acquainted with the newer advances in *Drosophila* genetics, to which he made a substantial contribution. On the other hand, he had a sarcastic manner with which he was likely to greet the more indifferent students as well as staff personnel in both Genetics and the office of the Dean of Agriculture.

During our early years of collaboration, I was often greeted by the students who said to me, "Dr. Stebbins, can't you get Dr. Green off our backs?" When I went away on sabbatical leave, I got echoes from the Dean's Office that Green's relationships with their staff personnel were far from satisfactory. Nevertheless, I still do not regret recommending him and in the long run feel that our relationship was well worthwhile. In particular, he was closer than I to the mainstream of genetics so that the course we taught alternately was greatly improved by his input.

My own book, *Variation and Evolution in Plants*, appeared in 1950 and was very well received. It was reprinted more than once and was still bought by students as late as the 1970s and 1980s. Rereading it now, I still find that its theoretical material stands up very well to recent changes, particularly those made necessary for teaching by the formulation of the Watson-Crick theory of DNA biology and the working out of the genetic code. When I was writing it, I had already become acquainted with the then-theoretical idea that genes are linear sequences of DNA rather than proteins, as all geneticists before 1945 believed that they were.

The implication of this new knowledge that did not become applied to plants until after 1970 had not dawned on me, and so I paid no attention to what were then only poorly supported theories. On the other hand, the development of the ecotype concept as carried out by Göte Turesson and the Jens Clausen school was, then and now, fully accepted except that the genic basis of ecotypes is now recognized as more complex than these earlier proponents had believed it to be. In particular, ecotypes rarely if ever are genetically isolated, even partially, from differently adapted populations.

On the other hand, the relationship between mechanisms for genetic recombination or its absence are now even better supported than in 1950. At that time, the distinction of prokaryotic organisms such as bacteria and blue-green unicellular photosynthesizers, and eukaryotic organisms such as protozoa and unicellular algae was not clearly defined.

The recognition that only eukaryotic organisms have well-organized chromosomes made possible the distinction between haploids, diploids, and polyploids. This raised the question, why are animals usually diploid except for their gametes while other eukaryotes

can be either haploid, diploid, or a combination of these states? The correlation that I emphasized in 1950—on the one hand between haploidy and relatively simple development, and on the other hand, between diploidy and more complex development—must still be emphasized, and the causal connection developed for this series of correlations. One of the most striking new discoveries is that among eukaryotes, the fungi are biochemically more similar to animals than to plants, particularly with respect to DNA. Hence, the correlations between haploidy and simple development in the lower fungi as contrasted to diploidy, the dikaryotic condition and the heterokaryotic condition in the higher fungi has evolved in association with selective pressures completely different from those exerted on green plants. Turning to the situation within the multicellular phyla of green plants, the correlation between haploidy and simple development versus diploidy and more complex development is so prevalent in distantly related groups that a causal connection between these conditions is difficult to deny, as I maintained in my book.

With respect to the phenomenon of polyploidy, the ideas developed in the book are now considerably better supported than they were in 1950. Following the adoption of the drug colchicine as a vehicle for doubling chromosome numbers, I decided to expose as many different autopolyploids as I could to the acid test of natural selection uninfluenced by artificial selection. I therefore planted, side by side, seeds of diploid and artificial autopolyploids of grass species and followed their changes in the semi-natural places where I carefully had planted them. Most of the plantings failed to yield any populations. Among those that initially gave results, only one species was successful enough so that I could make comparisons beyond the first generation that arose from the planted seeds. This species was the grass *Ehrharta erecta*, native to South Africa and already spontaneous in a small corner of the Berkeley campus.[1] Of the 10 sites in which I had planted seeds, only three gave results after the first generation, and in only one of them was the autopolyploid at first superior to the diploid planted beside it. Between the 10th and 15th generation, even this superiority disappeared, and in 1970, 26 years after the original planting, the diploid spread first over a few meters and later over 100 meters beyond the original planting while the autotetraploid was almost completely confined to the original area. This superiority of the diploid over the autotetraploid increased until 1984, 40 years after the original planting. From these negative results that included 10 different species, I concluded that a more or less homozygous self-fertile species, such as those I had planted, will rarely if ever yield a superior autopolyploid except after crossing with another differently adapted diploid race or species. Meanwhile, I had obtained data that contradicted the widely publicized hypothesis of O. Hagerup, that polyploidy induces greater resistance to harsh environments. In several different genera such as willows or *Salix*, sagebrush or *Artemisia*, and birches or *Betula*, and some species of *Iris*, the reverse is the case. Also, the initial evidence gathered from comparisons of chromosome numbers in various European floras is contradicted by comparisons of floras of Pacific North America where the highest frequency of polyploidy occurs in northern British Columbia, while central Alaska, at a considerably higher latitude and greater extremes of low temperature, has a lower frequency of polyploidy. The answer to this problem is obtained from knowledge of population structure as well as various external features of this environment, particularly the insular condition. For instance, in the large genus of grasses, *Poa*, diploids are known from above timberline in the western Rocky Mountains while the highest chromosome number in the genus, more than 200 chromosomes, is found in Auckland Island near the coast of temperate New Zealand. Apparently, under some conditions polyploids, because of their high degree of genetic

1. This grass, common around the Berkeley campus, is sometimes referred to as Stebbins grass by Berkeley botanists. — VBS

heterozygosity, permit the persistence of many genes in populations where their effects are covered by their dominant counterparts and can achieve a high degree of flexibility via recombination of both genes and chromosomes with the consequent controlled release of genetic homozygotes under conditions in which they have an adaptive advantage.

This hypothesis is strongly supported by artificial autopolyploids, which have been produced by Douglas Soltis in subspecies of the genus *Heuchera* (in Saxifragaceae). Soltis found a much greater frequency of heterozygous loci in the polyploids of the various species that were the object of his experiments. On the other hand, the relationship between karyotype morphology and evolution as described in Chapter 11 of my 1950 book, is still almost as poorly understood as it was when I wrote it.

This relationship is worth emphasizing because of the correlation between total DNA content and the adaptation to certain environmental conditions. As early as 1931, Nikolai P. Avdulov pointed out that genera of grasses adapted to temperate or cool climates have larger chromosomes than those that are adapted to tropical or subtropical regions. The same situation exists also in some legume tribes of Fabaceae. Furthermore, H. J. Price has shown that even within a single annual species, *Microseris douglasii* in the Asteraceae, a correlation exists between species or races that are adapted to relatively cool, moist regions and the lower DNA content of races adapted to warmer regions and also have somewhat shorter reproductive cycles. This correlation is to some extent reinforced by another correlation. In some cell cultures, higher DNA contents are associated with a longer mitotic cycle than species having a lower DNA content. Further experimental testing of this hypothesis in now possible in a number of plant species.

The condition that chromosomal differences are poorly correlated with and largely independent of ecological differences, as emphasized in Chapter 14 of my 1950 book, is still tenable.

An event that happened during the summer of 1950 is worth recording. I had just become separated from my wife Peggy and was living in Davis, while my daughter Edy had graduated from Carmel High School and was spending the summer in Berkeley before entering the University of Colorado in Boulder. She agreed to go with me to the Base Camp Session of the Sierra Club in the Lake Sabrina area west of Bishop. Shortly before we left, the secretary of the Sierra Club asked me if I would be able to take another passenger from Berkeley in my car. I agreed and was given his telephone number so I could arrange it with him.

The passenger answered very pleasantly, but added, "I hope that you can put some bulky plant presses in your car." As I pricked up my ears, he identified himself as a high school student, Peter Raven. On the way up to the camp, he explained that he was being helped by John Thomas Howell from the California Academy of Sciences and had been asked to put together a list of species found in the base camp area. When we got there, we discovered that single men like ourselves had been assigned sleeping quarters on a patch of beautiful green meadow close to the central area where meals were served. During the two-week period of the camp session, we explored together the vicinity of Dingleberry Lake where the camp was located.

Another visitor during the latter part of our stay was the eminent mountaineer and explorer of high peaks Norman Clyde. Because he was having difficulty with Oliver Kehrlein, the director of the session, I suggested that he might go with us on an overnight trip to Coyote Ridge, where several rare plants had been found. When we reached the summit of the ridge and looked at the particular locations of the rare species, Peter noted that they were all confined to a narrow strip of limestone that crossed the ridge.

At this, Clyde remarked, "Why don't you go to a mountain that has lots of limestone on it?"

"Where is that?" I asked.

"In the area of Convict Creek." I kept this information to myself for seven years until I had a chance to visit the area with my son Bob for rock climbing. I discovered that Clyde was right. In the same autumn of 1957, my colleague Jack Major told me about a graduate student of his who wanted to do a Ph.D. thesis by comparing a limestone ridge with one as near to it as possible that was underlain by granite. This triggered two years of research by Jack and his student, Sam Bamberg, and resulted in the discovery of a bog sedge (*Kobresia myosuroides*), new for California, as well as a small bulrush (*Scirpus pumilus*), both in the Cyperaceae, as well as several other species new to the area. Even more information came out of a problem that was uncovered in this area. The species of *Kobresia* is abundant in central Colorado where it grows on granite. The fact that it is confined to limestone in the Convict Creek area is therefore due to something else besides the difference between calcareous limestone and acidic granitic rock. We also noticed that in the area it occurs water seeps out from under the rock surface until midsummer, because the melting snow produces water that was trapped in cavities of the limestone. This shows that even the problem of restriction to limestone versus restriction to granite is not as simple as I and others had believed it to be.

As for my association with Peter Raven, both of us regard that summer as very important in our lives. Thirty years later, Peter was elected to the National Academy of Sciences and I accompanied him on his first visit to the sacred halls to sign the Academy's big book. I arranged that we share a hotel room in Washington for the occasion and asked him if he remembered when we had previously roomed together.

"Of course," he replied. "At Dingleberry Lake."

Chapter 20
In Search of *Dactylis* in the Mediterranean

From February until September of 1954, I took one of the most eventful trips I ever had. I was awarded a Guggenheim Fellowship to explore the populations of the orchardgrass *Dactylis* in the southern and southwestern Mediterranean region, where they are the most drought-tolerant perennial grasses that grow in the area. During the first four months, my headquarters was at the French University of Algiers, which was well established with a French chairman of its Botany Department, Marcel Guinochet. This was almost the last year that it existed as a French university, because the revolution that led to the independence of Algeria from France began toward the end of 1954.

I stayed in a modest hotel in suburban Algiers with a most welcome roommate, Åke Gustafsson, who had visited Ernest Babcock and me in Berkeley a few years earlier, and with whom I had become closely acquainted during the summer of 1948 at the VIII International Congress of Genetics in Stockholm.

Professor Guinochet greeted me most cordially and said that his colleagues and graduate students were looking forward to my lecture. I was a little hesitant about delivering it in French, but as this was my best foreign language and Professor Guinochet and others seemed to understand me well enough, I started in French and found that it went over well enough that I could continue in their language. I was, however, unprepared for French formality. Before the lecture began, the listeners had to be seated in two groups, with the faculty in front and the students behind in a circular aisle that separated the auditorium into two halves. After the lecture, Professor Guinochet asked for questions first from the faculty and then from the students, and it was only after the question session was over that I could descend from the podium and speak with everyone in the auditorium. Fortunately, however, there was plenty of time on the day following each lecture for me to hold informal discussions with students. The material that I presented was taken directly from my book, *Variation and Evolution in Plants*, which was made available to them and read by those who knew enough English.

Professor Guinochet was an authority on chromosome cytology of some members of the French and Algerian flora, but also very much interested in plant sociology. He followed the school of the Swiss ecologist Josias Braun-Blanquet, popular with European plant ecologists, which aimed to assign names to plant associations similar to those used by taxonomists for plant species. I was somewhat familiar with and somewhat skeptical of these techniques, and my enthusiasm for them was not heightened by what I heard at the University of Algiers. For instance, one of Guinochet's principal doctoral candidates and teaching assistant, Robert Gorenflot, was studying intensely the plants occurring on sea cliffs and beaches but paid no attention to the flora of the Algerian counterpart of our chaparral, which is called maquis. When I suggested to the professor that I hoped somebody was studying the maquis, he held up his hands and exclaimed, "The maquis, it is the ecologist's nightmare." This confirmed my suspicion that the methods of Braun-Blanquet had, with some success, been applied to plant associations that inhabit clearly defined habitats such as seashores, estuaries, and some bogs, but are inadequate to unravel the more complex associations of most forest areas as well as chaparral. When I got back to the United States and read up on the current literature of ecology, I realized that American and British ecologists had found similar difficulties and, in

general, found the taxonomy of plant associations misleading because of complex edaphic variation.

A further confirmation of this point of view came as a result of a detailed analysis of a plant association a few miles east of Algiers. Under Guinochet's direction, we made careful lists of species and assigned them to dominant or inferior positions in a hierarchy, but nobody mentioned an important fact that was plain to me: What we were studying was not even a seminatural association, but rather a group of weeds and other ruderals that had accumulated in an abandoned, formerly cultivated field.

The most exciting event during my stay in Algiers was a 10-day trip to the northwestern Sahara Desert led by Professor Guinochet, who was collecting material for his research and was assisted by a medical research worker, a specialist on snake and scorpion venoms. Fortunately, he was such an expert at this task that we hardly knew what he was doing, except when he told us about it. In three British Land Rover vehicles, driven chiefly by postdoctoral assistants, we drove southwest first to Beni Ounif, where we were entertained by the director of a small research station and from there Beni Abbes, which was dominated by an outpost of the French Foreign Legion. From there southward, we were in the almost trackless desert, which turned out to be quite different from what I had anticipated. Instead of sand dunes, date palms, and Arabs riding camels from one oasis to another, all we saw for about 100 miles was flat limestone pavement, completely devoid of vegetation as they were never wet because the scanty rain and dew seeped through cracks in the limestone slabs to subterranean aquifers. Right in the middle of this extreme desolation, one of the vehicles developed a mechanical difficulty that prevented it from starting. After the travelers had looked for every possible source of the trouble and had debated with each other over and over again, they gave up, attached the immobile vehicle to a stout cable on one of the other vehicles and started with a flourish to our next destination. This flourish was so strong that it brought forth a cascade of limestone pebbles that shattered the windshield of the Land Rover in which I was riding.

Nevertheless, we reached the desert station of Adrar safely and found a garage that was able to repair the damaged vehicle while we were able to see life in this desert haven and learn about the hazardous trip ahead of us, for about 250 miles to the southern edge of the desert. Fortunately, this was our southernmost limit, as there was a road junction from which we could return to Algiers by another route, which did pass through some of the Saharan desert dominated by sand dunes and palm-bordered oases.

The next morning we turned northeast with all three vehicles mechanically sound but with no replacement for the shattered windshield in front of my seat. I was assured that everything would be fine unless we ran into a sandstorm. We were only about an hour's drive north of Adrar when such a sandstorm broke. In front of us there appeared to be an impenetrable fog so that driving was possible but certainly hazardous. The only thing I could do was wrap a blanket tightly around my body, close my eyes, and cope with the driving sand as well as I could. This battle lasted for about half an hour until we had driven out of the storm area and were again in the calm of the desert. The French response to this relief was to stop by the side of the road and open a sack in which our medic had hidden a cooked desert partridge, which he had shot the day before while others were trying to repair the damaged vehicle. In another bag was a bottle of excellent red wine. We each received a sliver of the partridge and a small cup of wine with which we celebrated our recovery.

We then proceeded without difficulty to a remarkable oasis known as Timmimoun. This was much more than the traditional oases that were frequented by itinerant camel drivers. It was a desert town of about 4,000 inhabitants that had grown up around an opening in the limestone platform through which water was available from the aquifer below. Every flat area with any soil was planted in winter to barley (*Hordeum*) and in

summer to sorghum and other tropical cereal grains. We spent two very profitable days there, and were guided by a native of the town, a young man whose fluent and easily understood French helped us maintain contact with the Arabic-speaking villagers.

Our guide was very eager to have us look at the handwoven rugs made by the local people. He therefore introduced us to a salesman who spoke only Arabic. Those of us interested included myself, Åke Gustafsson, who was fluent in English but less so in French, a Danish graduate student who spoke good French and English, and a French young lady whose only foreign language was a modest English. Because each of us wanted to ask questions and give opinions in the language that we spoke most easily, we uttered for half an hour or more a babel of five languages: French, English, Danish, Swedish, and Arabic, all of which had to be funneled to the Arabic of our salesman via our Foreign Legion–based native guide. As each of us found a rug that seemed right as a gift or memento, the session ended happily for all. We were back in Algiers after an uneventful trip of two days.

My stay in Algiers was broken during the Easter holidays, when the university was not in session and I was eager to visit friends in Israel. I flew to Tel Aviv and was greeted by Michael Zohary, the father of one of my graduate students, Daniel, who was at that time in Berkeley. The elder Zohary was a professor at the Hebrew University and the principal taxonomist of Israel. In addition, he had made many discoveries of the adaptive values of local species, particularly in relation to seed dispersal. He was familiar with all of the localities for drought-resistant populations of *Dactylis* and guided me to many of them. My first excursion, however, was to southern Israel, the Negev Desert, under the guidance of another botanist, Naomi Feinbrun. We spent the night at a kibbutz that was the southern outpost of Israel and subject to raids from Arabs more or less continuously from 1948 to 1967, after which the southern area was occupied by Israel. Near this kibbutz was a dry streambed, or wadi, in which was growing the most drought-resistant of the orchardgrass races in *Dactylis* that I collected, being adapted to a desert in which annual precipitation was between 6 and 10 inches or 150 to 250 millimeters. Other orchardgrass strains collected in Israel were a diploid subspecies, *judaica*,[1] and several that were adapted to the northern part of Israel, where precipitation amounts were between 400 and 600 millimeters.

On another trip I learned about two kinds of difficulties that confronted botanists who were members of liberal Jewish groups. In one of the towns at the northern limit of the country, Professor Zohary and I got up on Saturday morning and were heading in our car for the area near the Sea of Galilee, when we heard a great clatter on a neighboring street. "We'd better turn around," Michael said. "Those people are orthodox Jews, and if they discover that we are preparing to work on the Sabbath, they will make trouble." He continued, "These days we have trouble from two directions, if we are in the southern part of our little country we have to be constantly on the lookout for raiding Arab bands, while here in the northern part we have to watch out for rigid orthodox members of our own religion and culture."

All in all, however, the result of my short visit to Israel was profitable in two ways; first I brought back seeds of highly valuable races of *Dactylis*, and second, I learned a lot about the struggles for independence of the recently born Jewish nation, and since then have been able to follow the fate of this nation through all of its later vicissitudes.

After the university session was over in Algiers, a junior member of the faculty, Louis Forel, agreed to guide me on a motor trip to the southeastern part of Algeria to a mountain range known as the Hodna Mountains where a rare relative of barley in the

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1. Stebbins and Daniel Zohary, Michael's son, later described the subspecies as *Dactylis glomerata* subsp. *judaica*, *Univ. Calif. Publ. Bot.* 31 (1959): 11. — VCH

genus *Haynaldia* was found on its slopes. To get there we drove to a small village from which Dr. Forel had arranged to provide horses and a member of the Forest Service as guide. The ride up the mountain was easy and the grass was abundant on the upper slopes. On the way up, an incident happened that reminded me strongly of a common dilemma that conservationists face when they are working in an area inhabited by people who are poor and have very different customs. While we were riding, our guide saw some people on the mountain, about a hundred yards away. He got off his horse, asked us to hold it and rushed to where the men were. His argument with them was fairly long and violent. When he got back to us, we asked him what the trouble was.

"They are stealing firewood against government regulations," the guide said. "The case is particularly bad because they are digging up a big stump and its removal will cause the mountainside to become eroded." Because I had seen a lot of erosion all over Algeria, I became sympathetic but nevertheless asked why they didn't know the regulation. He replied wearily, "Yes, they do, but they need the wood so badly for their home fires, both heating and cooking, that they dig it up anyhow and hope that they can get away with it." I asked what will happen to them, to which he replied, "They will go to prison."

"Have they been using this wood for fires for a long time?" I asked.

"Of course, it was the usual custom before we forest rangers came here to teach them about conservation," he said.

We spent the noon hour enjoying the cool green pastures near the summit of the mountain. Among the flowers common there was the brown bee orchid, *Ophrys fusca*, which according to a French botanist, Pouyanne, and a Swedish worker who studied the group intensively, is pollinated not by worker bees seeking nectar, but by male bees.[2] The structure of the flower mimics the structure of the abdomen of the female bee to such an extent that the male is induced to copulate with it, a process known as pseudo-copulation. I had read about this phenomenon in Berkeley, lectured to my students about it, and had seen the plants and the remarkable structure of their flowers during my sojourn at Algiers, but had never actually observed it. I explained my desire to my companions who were quite content to enjoy the coolness and calm of the mountainside while I satisfied my curiosity. I lay down near one of the flowers and waited. After a short while, I saw a bee, probably a male, dive-bomb the flower, grasp the lip petal, and go to work. Its jerky motions were suspicious, so after I had seen this several different times, I could be reasonably sure that I was watching pseudo-copulation. Our ride home back to the village and on to Algiers was therefore most satisfactory.

Soon after this banner day, I said farewell to my friends at the university and went by bus to Spanish Morocco and from there to Malaga, Spain. Another bus took me past a type of country that I didn't know existed in Europe, where donkeys were carrying bags full of sugar cane to a local refinery. Proceeding further, to Almería, I discovered growing on limestone ledges the snapdragon *Antirrhinum mollissimum*[3] that was obviously related to the ordinary garden snapdragon *A. majus* but extremely different in its low prostrate growth habit and strongly hairy leaves. I gathered seed, and at Davis the following winter, grew plants and crossed them to the garden snapdragon. The resulting hybrids were fully fertile and looked much more like the garden plant. I carried out one

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2. Pouyanne, A. "La fecondation des Ophrys par les insectes." *Bull. Soc. Hist. Nat. Afr. Nord* 8 (1917): 6–7. R. L. Dressler, pers. comm.

3. In the Scrophulariaceae, *Antirrhinum mollissimum* (Pau) Rothm. was published in *Feddes Repert. Beih.* 136 (1956): 66. This pubescent snapdragon is endemic to the province Almería along the southeast coast of Spain (cf. www.floresdealmeria.com). The plant taxon was later recognized as *Antirrhinum hispanicum* Chav. subsp. *mollissimum* (Pau) Fernandez Casas in *Candollea* 29 (1974): 332. — VCH

backcross generation and obtained progeny that were hardly distinct from the garden snapdragon. If I had not many other things to do and if this group had not already been examined carefully by Ernst Baur, I would have made a special study of this remarkable case of rapid evolution due to colonization of a drastically different habitat.

From this area, I went to the island of Ibiza in the Balearic Islands. I found that the limestone ledges there were covered by a small slender race of the orchardgrass *Dactylis* that turned out to be diploid and therefore one of the ancestors of the drought-resistant tetraploid. Before going on to Madrid, I spent a day on the island of Minorca, trying to find this same slender race, but neither in the field or in later careful examination of herbarium specimens from the much botanized Balearics could I find the entity that I named *D. glomerata* subspecies *ibizensis*.[4]

I went to Madrid intending to follow out my schedule of flying to the Canary Islands to find the most unusual race of orchardgrass in the entire genus *Dactylis*. However, when I woke up my stomach felt so queasy that I was sure a case of the disease known by some as "the Mediterranean trots," and by travelers in Mexico as "Montezuma's revenge" was upon me.

Nevertheless I had to keep up my schedule and knew nobody in Madrid to whom I could turn, so I went to the airport to catch the plane to the Canary Islands. Shortly after takeoff, I used for the first time the paper bag that is always provided for queasy passengers. I have never felt as low at any time on my travels as I did that morning. Here I was pale and sick and flying on a plane on which I knew nobody to a destination where I was an unknown foreigner. I could only hope that the hotel at which I had made reservations would contain somebody sympathetic with my plight. Fortunately, this hotel turned out to be a frequent destination of travelers from England, who usually went there in winter, so that in June when I arrived, I was one of a relatively small number of guests. The proprietor did everything he could to get me into bed and comfortable with a generous pot of tea. After a mealless evening and a reasonably comfortable night, my ambition returned and I thanked my host, giving him a generous tip, then took a bus that went across the island to the village Orotaba on its sunny southern coast. The cliffs along the shore were full of my orchardgrass. Instead of rising from a rosette near the ground, its inflorescences were on top of stems containing 20 to 25 nodes and looking like a miniature bamboo.[5] I explored a little more of the island during the next two days, but everything else that I found looked like an anticlimax. I therefore did no more collecting, as I was due to go to Morocco to join a group of botanists who formed a pre-Congress sightseeing tour with our ultimate destination Paris.

From the Canary Islands, I flew to Casablanca, Morocco, where I joined the botanists who had signed up for the pre-Congress trip to North Africa. Our guides were

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4. This subspecies in orchardgrass has been published as *Dactylis glomerata* L. subsp. *ibizensis* (Gand.) J. A. Rosselló and L. Sáez, but see also Stebbins and Daniel Zohary in *Univ. Calif. Publ. Bot.* 31 (1959): 12. The label from the Stebbins collection (*Stebbins 5477*, UC M003514) notes " … Island of Ibiza, 4 km NE of the town of Ibiza, in open maquis between pine forest and the sea, on thin soil over limestone ledges … ." The name was later realized as illegitimate and superfluous, with the correct name now *Dactylis glomerata* subsp. *nestorii* J. A. Rossello and L. Sáez, *Anales Jard. Bot. Madrid* 56 (1998): 396. Cf. www.ipni.org and TROPICOS, http://mobot.mobot.org/W3T/Search/vast.html. — VCH

5. Allozyme variation later explored this genetic diversity. Cf. J. Francisco-Ortega, A. Santos-Guerra, Seung-Chul Kim, and D. J. Crawford, "Plant genetic diversity in the Canary Islands: a conservation perspective," *Amer. J. Bot.* 87 (2000): 909–919. Herein, two endemic forms were investigated from a *Dactylis glomerata* complex: a "Canaria type," and the diploid *Dactylis glomerata* subsp. *smithii* (Link) Stebbins and D. Zohary, *Univ. Calif. Publ. Bot.* 31 (1959): 18, fig. 12. Cf. also W. Wetschnig, "Karyotype morphology of some diploid subspecies of *Dactylis glomerata* L. (Poaceae)." *Phyton. Annales Rei Botanicae* 31 (1991): 35–55. — VCH

well known to me and excellent, particularly Charles Sauvage, who had spent several years in Morocco. We first saw a little of the coastal flora and the maquis where the organizers had arranged that we see a harvest of the thick, rough bark of the cork oak *Quercus suber*. The corks that serve to stop our bottles grow in Morocco, central Spain, and Portugal. The bark is harvested every few years by cutting sheets of it away from the trunk. In this particular species of oak, the bark is so thick that removing a layer of it thick enough to make many cork stoppers leaves enough on the tree so that the wood and phloem of the tree are still protected and new bark can replace the old. From this exhibition, we drove to Fez, the largest of the ancient cities of the country, and had a fine chance to see Arabic culture in a form little different from that which has prevailed for centuries. We then turned inland toward our next destination, the high Atlas Mountains. We first stopped in the luxuriant forest of the Atlas Mountain cedar,[6] which was familiar to me from seeing several forests in Algeria and from cultivated trees that are scattered through California. Some of the trees were between 150 and 200 feet (45 to 60 meters) tall. The trip organizers had arranged for us a great feast or mechui. The entire feast was held in a huge tent. The tent was divided into five or six tables that were surrounded by six to eight cushions placed on the floor so that we could sit on them and reach the center of the table, where there was a succulent lamb that had been roasted over coals, supplemented by couscous, which is whole-grain hard wheat cooked as we cook rice. At each table was a French- or English-speaking leader plus a Moroccan chief who had supplied the food and could speak French and very often, English. There were no utensils. Instead, we were taught to use our three little fingers and thumb to grab a piece of meat from the roast and alternatively a small portion of couscous that we were supposed to dip into a bowl of sauce and roll with our fingers into a round ball, which we put into our mouths. One could use either hand. For me, extracting the meat from the roast was no problem, but with couscous, I was not able to make neat balls that didn't break apart, so that long before the meal was over there was a ribbon of loose wheat grains on the table between the bowl and my place at the table. After we had finished eating, the native music struck up and dancers appeared, performing a mild type of belly dance. All in all, it was a highly successful event for us.

From this forest we drove through scrubland with increasing numbers of interesting species all noted in carefully prepared lists provided to us. The end of the road was at the mouth of a wide ravine leading directly to the summit ridge of the Atlas range. We stayed there long enough so that I could climb well up on the ridge and get an idea of the subalpine flora. I have never before or since seen such a desolate example of a high mountain flora. There was evidence that for centuries sheep and goats had repeatedly grazed there, and the fresh tracks and living animals were donkeys and camels. The whole ridge was covered with xeric or dry land vegetation of which the most common species was a perennial species of locoweed or *Astragalus* from the legume family. There were no woody plants at all on the ridge over which I was walking at about 9,000 feet, although I did see a few scrubby juniper bushes on an adjacent ridge. The whole agony of a destroyed high-altitude plant community brought forth in me a paraphrase of one of the verses of Coleridge's "The Rime of the Ancient Mariner."[7]

> All those lovely mountain flowers,
> 'Twas sad for them to die,
> And a hundred thousand spiny things,
> Lived on and so did I.

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6. The striking Atlas cedar, *Cedrus lebani* A. Rich. — VCH

7. This paraphrasing was taken from "The Rime of the Ancient Mariner" (1798) by Samuel Taylor Coleridge (1772–1834). — VCH

I believe that some of the less frequented parts of the Moroccan Atlas have a fairly rich flora, but we didn't see it.

From this last excursion, we returned to the airport and flew to Paris for the Congress.[8] As to be expected in France, this was a relatively easygoing affair and many of us enjoyed the sidewalk cafés almost as much as the scientific proceedings. My talk on speciation in relation to chromosomal change, abstracted chiefly from my 1950 book, which the audience didn't yet know, went over quite well.

During the Congress, I talked again with two old friends from Austria, Karl Rechinger and Friedrich (Fritz) Ehrendorfer. I invited them to accompany me on a motor trip through Spain and northern Morocco, which they happily accepted. I then made contact with my son Bob, who had just arrived from California, and together we left Paris in a car that I had rented, heading for the Pyrenees Mountains, which we crossed, and drove on to Madrid. When we got near the crest of the Pyrenees, we looked for a good mountain to climb and found one that turned out to be not too difficult at all, but still a challenge for a rope and pitons that Bob had brought with him. However, halfway up the mountain we were chagrined to discover ourselves out-climbed by nature.

One of the most famous mountaineers of Europe, the chamois,[9] which is related to our Rocky Mountain goat, dashed up from just behind us and in a few graceful bounds, reached the summit of our ridge, which required a half-hour climb for us to reach ourselves, where it disappeared over the top. I have occasionally seen these animals in other parts of the Alps and always stare in wonderment at their phenomenal ability to bound from one crag to another.

When we reached Madrid, we met Karl and Fritz at our hotel as planned. After two days of sightseeing, we continued southwest to Córdoba, stopping on the way to collect chiefly the rarer species of thistle. Apparently, the wing of the herbarium in Vienna that contained the largest collection in Europe of these plants had been destroyed during the war by a bomb, and Rechinger's main objective was to replace as much of this loss as he could in a single trip. From the southwestern corner of Spain, we crossed to Tangier in northwestern Morocco and met a friend whom we knew from Carmel, California. He gave us helpful suggestions on how to reach the northern mountains of Morocco, but commented that they looked pretty barren to him and he doubted that we would find very much. He was right. Again, the mountain ridges were so highly overgrazed that we found only a few widely separated patches of maquis and open woodland. These turned out to be cemeteries that we knew we had to avoid because it is sacred ground on which no infidel should tread. We therefore went back to Spain and spent several days at Granada. This was one of my major objectives, as a high mountain range, the Sierra Nevada of Spain, rises from the city to well above timberline, and on its higher slopes is a mountain hotel. This was excellent in the long run for my collecting, but at first created problems.

In Spain, the regime of the middle and upper classes that includes dinner after 9:00 in the evening and breakfast at 9:00 to 10:00 the following morning is upheld in the mountains as well as elsewhere. After some persuasion, we arranged that they put on the side table of the dining room, both a breakfast for us to eat at 7:30 a.m. before any of

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8. The VIII International Botanical Congress was held in July, 1954, in Paris, France. Stebbins' book referred to his *Variation and Evolution in Plants*, 1950. — VCH

9. The Pyrenean chamois is the mountain goat known as *Rupicapra pyrenaica* Bonaparte and found from northern Spain to the Apennine Mountains in Italy. It is regarded as a species distinct from *Rupicapra rupicapra* L., more broadly distributed in Eurasia. Their American equivalent is *Oreamnos americanus* Blainv. Cf. D. E. Wilson and D. M. Reeder, eds. *Mammal Species of the World* (Washington, D.C.: Smithsonian Institution Press, 1993). http://www.nmnh.si.edu/msw. — VCH

the cooks or servants would arise, as well as lunches that we could take in our backpacks and eat on the mountain. The road from the hotel to meadow areas at about 10,000 feet (3,000 meters) was a bit rough but without major difficulty. There we found abundant populations of *Dactylis juncinella*,[10] and their seed was ripe for harvest. We later determined that it is another diploid that is not far in geography from the Balearic race *ibizensis*[11] but totally different in its climatic and edaphic adaptation. In this latter respect, it is also extremely different from the diploid that I had collected in the Canary Islands.

Returning to Granada, we bade good-bye to Karl Rechinger, who had to get back to Vienna. We went on northeast about 100 kilometers to a small town just north of an eastward extension of the Sierra Nevada, which according to a geological map was underlain by an acidic rock formation. This was very important, as nearly all of the other Mediterranean populations of *Dactylis* were underlain by limestone or other calcareous rocks that are rare in the California Coast Ranges and foothills. We had not made reservations at the local hotel, because none was listed in our guidebook, but Fritz had assured us that any town big enough to be on our map would have a hotel. This was true for Purchena, but we were out of luck for another reason. A large theatrical company from Madrid had arrived the day before and had taken all the rooms as well as the interest of the population. After cruising around the town and asking many questions, we finally found a generous lady who had spare rooms for the three of us overlooking a little plaza from which we could see the townspeople getting their water and chatting with each other. All was well until I had to use my somewhat inadequate Spanish to find out where there was a restroom, as we didn't see any near our bedroom. The cheery reply was, "Hay el campo" (down there we have our fields), a direction that we followed as judiciously as we could. Such directions are absent from all tourist guides because the kind of place that I had to visit to find my plants is not listed in guidebooks.

The next day, Fritz Ehrendorfer also had to leave for Vienna so that my son Bob and I were by ourselves. On driving south to find the expected acidic rock formation, I discovered that either the map was wrong or I had misread it, as the soils on this mountain ridge did not appear to differ from many other places we had visited. Bob and I therefore headed east, visiting first the city of Valencia and the village Sagunto, a few miles to the north. This village was at the base of a high cliff that has been fortified ever since prehistoric times. It displayed clearly a marked succession of different cultures. At its very top, there were basins of rock that had been apparently used by the ancient inhabitants. Later, fortifications were built to protect this high ground from the Romans about the time of Christ. The descendants of the Romans were themselves conquered by the Arabic Moors several hundred years later, so that some of the fortifications had a distinct Moorish character. The recapture of Sagunto in the Middle Ages led to the construction of fortifications that could resist cannons. Finally, the most recent fortifications were of a 19th-century character, because they were built by French armies during the Napoleonic invasion.

We continued onward toward the French Alps, where we hoped to do some rock climbing. However, when we arrived near the border between Spain and France in the city of Tarragona, Bob came down with a violent case of digestive disorder with a high fever, so we had to stop to give him a chance to recover. Our hotelier was most sympathetic and guided us to a hospital run by Catholic nuns. They also received him gladly

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10. Bory's species *Dactylis juncinella* was later reduced in rank by Stebbins and Daniel Zohary as *Dactylis glomerata* subsp. *juncinella*. *Univ. Calif. Publ. Bot.* 31 (1959): 13. — VCH

11. Stebbins' *ibizensis* (published in 1959 with Daniel Zohary as a subspecies of orchardgrass) was correctly named *Dactylis glomerata* subsp. *nestorii* J. A. Rossello and L. Sáez in 1998. — VCH

and charged only a modest fee, and Bob got all the care that he needed. I was really surprised to find how, in such strange places, we Americans could be so well treated.

We finally got to Chamonix at the foot of Mont Blanc, and also at the foot of the most exciting rock climb in western Europe. The weather was bad and had been so for several days. The best we could do was to practice ice climbing on a glacier while hoping that good weather would arrive. Unfortunately, we had reservations for separate return trips out of Paris that made it necessary for us to leave Chamonix a day before acceptable weather returned. Bob then went back to his studies at Colorado State University, Fort Collins, while I returned to Davis to sort out a big pile of mail and continue other work that had been delayed for eight months.

My first year of research after the African trip enabled me to count chromosomes of my accessions and make plans for the future. Two bright prospects had already come to me and a third was to come after my preliminary experimental work. First, I had in my garden living material of 10 very different *Dactylis* and knew about two or three other possibilities. These diploids were highly distinct from each other and if it were not for the tetraploids, each one of them would qualify as a distinct species. Furthermore, they are widely separated from each other geographically and ecologically. Second, all hybrids made between different ones of them were vigorous and fully fertile. Wherever later generations were produced, their plants were also fertile. The pattern of distribution of diploids and tetraploids was highly interesting. All but one of the diploids were highly restricted, the only one widespread being *ashersoniana*, which was already well known from central Europe, while its close relative named subsp. *himalayensis* would be united with it if it were not separated by such a wide distance from *ashersoniana*.[12] All of the relatively rare subspecies were localized in peripheral regions of the complex as a whole, such as northern Iran, Israel, western Algeria, the island of Ibiza in the Mediterranean Sea, the Canary Islands in the southeastern Atlantic Ocean, the high Sierra Nevada of southwestern Spain, and the coast of Portugal. All of the territory between these extreme outposts is occupied by the very common, almost weedy subspecies, including the desert lovers that I collected from Israel. The genus as a whole is a perfect example of a polyploid pillar complex like the one that I had already suspected to exist in *Paeonia* as well as in the American species of *Crepis* and the perennial species of *Bromus*. It seemed to me that all I had to do with this material was to produce hybrids between diploids, tetraploids, and each other, and then to give a chance for natural selection in California habitats to extend the complex to form valuable forage grasses for lowland California. *Dactylis* seedlings from artificial hybrids from different tetraploids were successful in some natural plantings. I therefore selected a favorable garden area and planted in it clones of the most promising genotypes and showed the plot to my agronomy-trained colleagues. They at once realized that the seed heads would be very difficult to thresh in such a way as to recover a maximum yield of seeds. They said that even though we might get a highly adaptive new hybrid variety, the additional reward as compared to use of well-known varieties under partial irrigation, which had then become possible due to the increased supply of water that had arisen from the large, recently constructed dams, would not be economically rewarding. Here then, was the end of the trail. Fifteen years of research carried out on four different genera on a broad scale resulted in possible success in producing a new hybrid drought-resistant grass, but converting the genetic hybrid populations to agronomically suitable races for

12. Both subspecies had been described earlier in the 20th century as *Dactylis glomerata* subsp. *aschersoniana* (Graebn.) Thell., *Allg. Bot. Z. Syst.* 7 (1911): 34; and *Dactylis glomerata* subsp. *himalayensis* Domin, *Acta Bot. Bohem.* 14 (1943): 129. — VCH

use by ranchers was still a will o' the wisp that eluded me. I decided to accept the reward that had come to me through greater knowledge of the cytogenetics and evolution of the grass family, and to turn my attention to other problems of plant evolution that might offer better rewards.

Chapter 21
Geneticists in Japan and Transitions at Davis

In 1956, I had a short visit to Japan. The IX International Congress of Genetics had authorized the geneticists of Japan to organize an international symposium to take the place of a Congress more typically held in Europe. Among the best-known geneticists who attended were Professor J. B. S. Haldane and his wife, Dr. Helen Spurway, from University College, London, England. I was asked to attend and to give a talk on chromosome changes in grasses, with particular attention to the difference between rice and the northern grasses. At that time, I had just finished a long review article on hybrid sterility and inviability in both animals and plants. By good fortune, one of the very first talks given by others was by Dr. Spurway dealing with the same phenomena in certain species of fishes and amphibians. I therefore asked her if she could take my manuscript, read it during the session, and return it to me with comments, particularly to make sure that I had not left anything out on the animal side. She was delighted to do this and said she would see me later. This opened up a brief relationship with Dr. Spurway upon which I capitalized at other times during the symposium.

Professor Haldane and Dr. Spurway were conspicuous at the symposium because they always stayed together and appeared to many participants to be somewhat rude and arrogant, particularly to the thoughtful and gentle guides who had been delegated to help us with problems in an unfamiliar country. I next had an opportunity to talk to Dr. Spurway by herself during an organized holiday that consisted of a train ride to a famous shrine north of Tokyo followed by a visit to a nearby mountain lake and experimental station for fish genetics. On the train trip from Tokyo to the shrine, we rode in typical Japanese passenger cars, which like those in England, were divided into separate compartments, each of which held five or six passengers. In our preliminary conversation, I became used to her voice, which according to another geneticist, "had all the delicacy of an iron file rasping through a steel bar." I decided to pick up a little history and asked her when she and Dr. Haldane had become married. I knew that she was at least his second and perhaps his third wife.

Her answer was quick and succinct. "I became his mistress in 1943 and his wife in 1945."

When we had finished our sightseeing at the shrine, we got into buses for the drive to the mountain station and I found myself with another interesting pair of geneticists. Eight years earlier, in 1948, the Russians essentially declared war on what they termed "reactionary Mendelism-Morganism" and substituted their new genetics promulgated by Trofim D. Lysenko. Its principal belief was that the permanence of genes was a bourgeois myth and that the proper handling of the environment could reduce any adaptive differences that orthodox geneticists ascribe to mutation and Darwinian selection. After one or two European geneticists had visited the Union of Soviet Socialist Republics and had tried to find factual support for Lysenko's ideas, they were convinced that it was completely fraudulent, and two books had already been published refuting this. Consequently, the attendance at this Japanese symposium of two Russian Lysenko proponents was a matter of great interest, and we conversed with them as often as we could to form our own opinion. I had a chance to do this on the drive from the shrine to the mountain lake. When I was sitting next to one of them, Dr. Ivan E. Glushchenko, I looked at the fine forest of the conifer, *Cryptomeria japonica* (Japanese cedar), and remarked that Japanese

foresters were to be praised for maintaining such a lifelike forest from an artificial planting.

Glushchenko retorted, "That forest isn't artificial, it must be natural."

As I had on the previous day had a long walk with a Japanese botanist through a similar forest, I could maintain my stand. "All you need to do is look carefully and you will see that the conifers are arranged in straight rows," I said.

He was at first unwilling to do this, but as soon as I pointed out one row after another, he finally became convinced. When he had first made his remarks, he was so aggressively positive about his position that his dogmatic nature glared at me. He seemed to be a long way from the traditional unbiased scientist who puts observed facts ahead of theories based on general expressions.

After about five days in Tokyo, the symposium was scheduled to move to Japan's second intellectual center, Kyoto, and to spend the night on the way at a large hotel where we were supposed to obtain fine views of Mount Fuji that had thus failed us because of persistent clouds.

At dinnertime that evening, Dr. Spurway said, "My husband and I have read and studied your manuscript and would be much interested in talking with you about it after dinner." We therefore spent quite a lot of useful time in the evening in the barroom with steins of beer and the manuscript.

The principal session at Kyoto was a general one in which the major participants presented their views about the status of genetics. Before the afternoon session, I had lunch with Helen Spurway Haldane and witnessed a particularly striking example of her abrupt attitude.

At the end of lunch, one of the female guides came up and said to her very gently, "We have arranged a particularly interesting program for the wives of the participants so that you can get a good idea of what Japanese homes are like."

Helen snapped back, "Please leave me alone, I have to stay and listen to my husband."

When we were all seated for the afternoon session and Haldane got up to speak, he made his usual uncomplimentary remarks about American capitalists, even though the American committee had provided the funds for his presence at the symposium. Helen froze and grabbed my hand. "Please hold my hand tightly, this is going to be awful," she gasped out.

Apparently, throughout the symposium, she had been in a state of nervous tension because of his remarks, even though she was not much better herself. All in all, the symposium was highly successful and when the announcements were issued for a full-fledged International Congress of Genetics in Tokyo in 1980, those who had attended in 1956 looked forward eagerly to this Congress.

In the following year, 1957, I was invited to another meeting that later affected my life a great deal. The Indian plant breeders, as part of a celebration of the anniversary of their day of independence, held an international symposium of genetics, evolution, and plant breeding. Its international character was based on the presence of more than 40 Indian plant breeders, four breeders from Pakistan, and three from the rest of the world. They included my old friend from Sweden, Åke Gustafsson, another old friend, Otto Frankel from Canberra, Australia, and myself. Each of the three of us presented to the graduate students short summaries of our research interests as they affect plant breeding and listened to their questions and comments.

Just before leaving the United States, I had received word from the Foreign Affairs Office of the Rockefeller Institution that if I submitted to them the names of three foreign students, they would consider granting scholarships that would permit these young men to come and work for their Ph.D. degrees in our department. I was therefore on the

lookout for the most promising candidates and submitted to the Rockefeller office three names, Subodh Kumar Jain, Surya Kant Shaw, and Gurdev Khush. They were all accepted and arrived in Davis in the autumn of 1958.

Mr. Jain did not care much for the topic that I suggested that he work on in cultivated rye and its relatives. On the other hand, he showed unusual mathematical ability and became immediately interested in the course he was taking under my colleague Robert Allard on population genetics. I therefore asked Bob if he would take Jain over as a Ph.D. student and found him quite agreeable to this proposition. Jain performed so well under Dr. Allard that shortly after receiving his degree, he was appointed to the Agronomy Department at Davis and eventually became a full professor, a position from which he retired as emeritus.

Surya Shaw was much interested in a topic connected with my own new interest in development, dealing with patterns of interaction between cells during the development of the epidermis of barley and other grasses. Upon receiving his Ph.D., he returned to India and soon afterward became principal plant breeder in the Indian sugar research experiment station.

Of the three, Gurdev Khush had the most outstanding career. After getting his degree with me on the cytogenetics of rye, he accepted a postdoctoral position with my colleague Dr. Charles M. Rick and did excellent research on monosomic (trisomic) genotypes, which was published in a small book, *The Genetics of Aneuploids*. He then became chief plant breeder at the Rockefeller-supported International Rice Research Institute at Los Baños, Philippines. His task was to make better use of a newly discovered rice genotype, which had been first designated as a "miracle variety" but had fallen into disfavor because, in spite of its superior productivity, its agronomic uses were too limited. Khush assembled a group of Asian plant breeders as assistants, and he used the method of backcrossing and selection. He put the valuable quality of this variety, which has short, stiff stems and a higher branch number, leading to a much greater number of seed heads per plant, on the genetic background of varieties adapted to various edaphic conditions and likewise a variety of grain qualities that affect stickiness and other properties after cooking. This aggregation of "miracle" rice varieties has become standard for Southeast Asia and has increased yields to such an extent that the East Asian nations that formerly had to import rice to feed their populations are now exporters of rice to other tropical regions. Khush's success attracted the attention of plant breeders throughout the world so that he received a prize that is sometimes regarded as the nearest approach to a Nobel Prize that plant biologists can win. It is called the Japan Prize, because it is awarded by a committee of Japanese plant biologists.

Obviously, I feel that my selection of the three plant scientists whom I was able to bring from India to our university has paid off well.

To me, at this late date, the honor that my former student Gurdev Khush received is most satisfying. My attempt to use grass cytogenetics to improve human food resources did not pan out. I never came near winning a Nobel Prize, although nonprofessional friends have occasionally asked me why not. The fact that one of my Ph.D. students has come as near as any plant scientist can get to achieving a top international honor has compensated for my own inadequacy in this direction.

My first 15 years in Davis formed a transitional period in my life in every respect. First, with respect to teaching, I had already guided the Ph.D. program for 12 students but in addition, three more students were still under my direction, even though they were finishing their work in Berkeley. This meant frequent trips back and forth from Davis to Berkeley. With respect to coursework this was also true. The Berkeley department was unhappy with the sudden change in teaching my advanced course in Darwinian evolution, so that I looked for a way to continue teaching it there, while at the same time fulfilling my teaching duties at Davis. I found this possible by teaching beginning

genetics and evolution courses in Davis on Mondays, Wednesdays, and Fridays, and going Tuesdays and Thursdays to Berkeley to give two lecture-discussion sections on each of these days. I kept up this alternation for 16 years, and enjoyed doing so, but decided in 1966 that I would give up my connections with Berkeley.

In Davis, I shared the Beginning Genetics course with Mel Green until 1960, when Dick Snow could be persuaded to take it over. One reason for this change was that a group of biologists, chiefly in the Zoology Department, were collaborating with faculty members in other fields of science to provide an academic major or at least an orientation in integrated studies. They pointed out to me that undergraduate biology majors did not have time to reflect on what they were learning. In the beginning course, they were too busy learning terms and doing routine laboratory work, while after this introduction, all of the courses biology majors took were specialized so that they graduated without understanding the meaning of much that they had learned. I and others suggested that a course could be organized and designed particularly to fill this gap, and they asked me to follow up this suggestion. I did so by offering a course that consisted of multidisciplinary problems in the field of biology. Some problems were theoretical, such as the energy cycle or the nature of reproduction, while others were more practical, such as an introduction into the biology of cancer and the problems of epidemiology. The schedules of the students were such that the course could not be required for all majors as I would have liked to propose, but nevertheless it was reasonably popular and reactions of students permitted me to feel that it at least in part obtained the desired integrated result.

Another activity that was important to both campuses was preparing a textbook for the evolution course. Of the two books that were already available and sufficiently modern, Dobzhansky's *Genetics and the Origin of Species* paid too much attention to *Drosophila* and too little to ecological factors and to plants. On the other hand, those of Ernst Mayr, G. G. Simpson, and myself were too specialized in other directions. I therefore wrote a book requested by Prentice-Hall publishers that included examples from all of these works, with particular emphasis on topics that included an elaborate account of Darwinian natural selection, such as mimicry in butterflies as analyzed via data on population genetics and Darwinian natural selection. This book, titled *Processes of Organic Evolution*, was highly successful and went through three editions.

My election to the National Academy of Sciences in 1952 opened the way to yet another activity. A fellow botanist who had been elected to the Academy a few years earlier asked if I would take his place on a committee called the International Union of Biological Sciences, connected with the organization UNESCO of the United Nations. This turned out to be a cozy little group of French, Italian, German, and English biologists who were able to make small grants to scientists in various countries. Soon after my election, the group decided that biologists should stage a counterpart of the International Geophysical Year. Longer periods of research for such a program extending over several years appeared to be more appropriate than a single highly publicized year. This brought about the International Biological Program (IBP) that lasted for several years but, for various reasons, later declined and disappeared. One reason was too much politics, particularly in organizations sponsored by the United Nations. Another was a split among the promoters of the IBP program as to where the scientific benefits would be most rewarding. I felt that this world-publicized program would provide unusual opportunities for scientists in smaller countries and the larger developing nations. The majority of the promoters, however, believed that the progress of science would be best served by using the publicity to promote projects of global scope designed and carried out by leading scientists in the more developed countries. Even now, I am still uncertain as to which avenue would be best. At any rate, my activity with the IBP and the similar

but broader International Council of Scientific Unions (ICSU) has been my only public service committee work.

Additional transitions took place from 1950 to 1958 in both my personal life and my own research program. After my first wife Peggy and I had been separated for a year, we both felt a little unhappy over the situation, particularly with respect to our third offspring George, who during this period was in his late teens and early 20s and still under our charge. We tried various alternatives for living together, but finally she couldn't take either the heat or the social life of Davis and wished to spend the rest of her life in the cool, quiet atmosphere of Carmel. So we were divorced. I was therefore definitely without a mate and looking for one.

I found a friend whom I had known casually for several years, Barbara Monaghan, who had been divorced and was raising a son whom I first met when he was seven years old. After a brief courtship, we were married in 1958 and remained so until her death in 1993. During this time, we had our not-unexpected ups and downs and managed to see our son Marc grow up, graduate from Berkeley with top honors in geology, earn a Ph.D. at Yale, marry, and produce two grandsons. Meanwhile, my older son, Bob, and my daughter, Edy, both married and produced offspring, so that I now have from my marriage with Peggy seven grandchildren and nine great-grandchildren.

In this connection, the greatest tragedy of my life was the suicide of my son George in 1969 at the age of 34. He was living alone after getting his degree at Reed College and his master's degree at Sacramento State University and was working as a social worker in Los Angeles. I am at a loss to explain it.

Chapter 22
Mountaineering with Bob

My joint mountaineering excursions with my son Bob have been much more than just the outings themselves, even though these were among the most enjoyable hours I have spent in my life. The intimate relationship we established and fortified during these trips is, I believe, very unusual and perhaps unique for a father and his son.

From my boarding school days, I have taken many wilderness excursions by myself, and during college and graduate school years my principal recreation consisted of excursions with friends such as Dick Dow and Al Currier as well as organized groups such as the Harvard Mountaineering Club and the rock climbing section of the Appalachian Club of Boston. I also took modest excursions with Bob when he was a boy. When he came home from Colorado State University for his first vacation, I was delighted to learn that he had become very active in their mountaineering club and with them had climbed the precipitous east face of Long's Peak in the Rocky Mountain National Park. From this experience, he had learned techniques of climbing with ropes and pitons that were not yet available when I climbed during my college years. I knew also that he was very sensible and against taking any risks, however small. Furthermore, after I had separated from Peggy, I was free and alone during the summers and could not imagine any better association than that with Bob.

Our first excursion, before Bob went off to college, was in the Big Sur Canyon area of the Santa Lucia Mountains south of Monterey and Carmel. One of the highest peaks is Ventana Double Cone, which has a gentle north-facing slope with a trail leading to a fire station at the summit. In contrast, the south-facing slope is precipitous and from the Big Sur Canyon to the south is an inviting target for ambitious rock climbers. Both with and without Bob, I had made several exploratory trips from which I realized that in order to climb the south face successfully, one would need to camp overnight near the headwaters of Ventana Creek just below it. The hike from the bottom of the Big Sur Canyon where it meets Ventana Creek up to the campsite is itself exciting because there is no trail and the lower part of the canyon is so narrow that, in one place, one must wade along the creek, holding one's pack overhead. The fern-draped side walls and the lofty redwood trees rising above the canyon are themselves magnificent, so that this canyon is a spot of solemn beauty where anyone can leave the bustle of central California and have the whole visible world to oneself.

On the critical day of our climb, we passed through this beautiful spot with little delay, as our minds were fixed on the climb scheduled for the following day. In order to be sure that we could make it both ways during the day, we had a quick breakfast and started to climb at about 6:00 a.m. To our surprise, the cliff was easily negotiated without climbing aids, and we reached the summit of the mountain in about three hours. We were both very casually dressed. As we approached the fire tower, the warden on duty greeted us and exclaimed, "Where did you two come from?"

"From the bottom of Ventana Canyon," I replied.

He grinned and remarked, "Well, you two boys must have had quite a climb." This was one of the most complimentary remarks I had ever received. I never imagined that I would reach the age of 44 and be confused with a six-foot son, aged 17.

During Bob's freshman and sophomore years at Fort Collins, I attempted a reconciliation with Peggy that did not turn out, so that in June of 1953 I was again alone.

During that summer, Bob was employed in a lumber camp in the Sierra and had time off for two trips during weekends away from his job and a third when his job was over. For the first of these, we went to Fallen Leaf Lake on the southwest margin of Lake Tahoe where my whole family had spent the summers of 1939 and 1940. During the latter summer I had taken Bob, then age seven, on his first climb with me at Angora Peak. Just opposite Angora Peak is a prominent cliff called Indian Rock and another in the same vicinity known as Cracked Crag. Both of these turned out to be interesting and not difficult rock climbs during which we could reminisce about our earlier summers in the area.

In midsummer, we took a long weekend excursion to the east side of the Sierra, below Mount Whitney, that we thought we might attempt by the rock route that the Harvard Mountaineering Club had explored in 1932. In order to be away from other climbers, we took a fisherman's trail from the road head to a meadow between the north side of Mount Whitney and the southeast side of Mount Russell. We first climbed Russell, which was easy but necessary in order to get ourselves ready for the more strenuous ascent of Whitney. When the day came for the big climb, the north wind was so strong that I was afraid we would be blown off the mountain if we tried the difficult east face ascent. We therefore climbed the mountain by the north face over the John Muir Route. When we reached the top, other climbers, including an eight-year-old girl, had arrived via the mule trail that ascends the southwest side of the mountain. We were not ashamed of being second to a child, but enjoyed the pleasure of an acquaintance with others who had the same ambition we had.

In 1955, we hoped to climb the east base of the Middle Palisade in the Palisade Glacial Basin. However, when we got there, we discovered that the usual cascade of boulders that fall off the mountains early in the season had lasted longer than usual, and the gullies, which were the only approach to this side of the mountain, were highly exposed to falling rocks and definitely unsafe. We therefore accepted a consolation prize of Cathedral Peak, which is formed by a large spur jutting out from the main crest. This turned out to be a good climb and not very difficult.

We then turned our attention to a peak on the Sierran crest that is just north of the North Palisade, known as Mount Winchell. It had been climbed from the west as well as from the east but not from the north. We therefore looked for a route on that base, which turned out to be possible with some difficulty but no insurmountable problems. This definitely was a new route that could be reported to the Sierra Club's rock climbing section. Before leaving the mountain, we drove to Lake Sabrina with a view toward finding a new route up one of the surrounding peaks. We hiked up to North Lake, and when we got to about 9,000 feet, we camped there. Early the following morning, we hiked up the trail toward Piute Pass and our eyes were struck by the beautiful granite slabs that form the precipitous south face of Mount Emerson. This looked like real fun and we set about it. Climbing the slabs to the crest of the east ridge was, for us, near the limit of our capacity, but the rock was firm with plenty of belays for pitons so that we reached the ridge crest in good time. However, the ridge looked formidable because it was very narrow and had precipices several hundred feet high on either side. Finally, the crest became so narrow that we could no longer walk on it and the sides were remarkably deficient in footholds. After some debate, I reminded Bob of a method that climbers in the Alps use for negotiating successfully such situations. This was to straddle the crest of the ridge as if it were the back of a horse, pushing ourselves forward with our legs dangling down toward the precipices that lay on either side. Bob started out from the last belay point about which I could anchor his rope and continued for about 30 feet while I let the rope out from the belay. He then found a suitable belay point and asked me to follow him. We were both successful and could then continue along the slightly broader crest until we reached the summit of the mountain at 13,300 feet in altitude.

The descent of the southwest ridge was hardly more than a scramble. This climb was by far the most exciting one that we tried.

Flushed with success, we decided to stay another night at our campground on North Lake, and on the following day we decided to move our camp to another location east of Mount Darwin. While in this area with the Sierra Club in 1950, I had often looked at the east face of Mount Darwin, which is formed by a series of granite slabs over which I had a violent altercation with Oliver Kehrlein, the leader of the Sierra Club trip. He insisted that the slabs were so steep and slippery that climbing over them would be dangerous, while to me they seemed less precipitous and traversed by cracks wide enough for our feet and probably provided with points of rock for belays.

Here again, five years later, I decided to test our alternative hypothesis, and if I was right, to work out a new route for climbing the mountain bearing the name of Charles Darwin, my evolutionary hero. Consequently, after a day of rest, we started for the big mountain. Below the slabs the mountain presented another barrier consisting of a nearly vertical but highly fissured set of crags. We roped up at the bottom of one of these, and Bob started looking for a route while I was belaying him. Everything went very well until we were almost over this barrier. Then a freak accident happened. Bob was about 30 feet above me and the rope between us rested in one or two places on narrow flat ledges. Apparently on top of one of these ledges was a pebble a few inches long with sharp edges. As Bob was climbing and exploring, he dislodged this pebble about five feet below him and it came bouncing down toward me. To make a big move in order to avoid it, I would have been forced to let go the belayed rope leading toward Bob. As luck would have it, the pebble bounced right into my hand with such force that it tore open my index finger, which started bleeding heavily. I had to use a handkerchief to staunch the bleeding. Obviously, I could not proceed without having it well bound up. I had to ask Bob to climb back down to me and look it over. We both agreed that it needed more attention than we could give it ourselves.

We climbed back to our car and drove down to Bishop about 15 miles away. The surgeon at the hospital there had to stitch my wound up so that my climbing days were over until it healed, which it fortunately did without complications. Nevertheless, the safest course was for us to go home so that my injury could receive continuous care. I was hoping that during the next year or two we could make another attempt on this route, but we did not get another chance.

A few years later, I was reading a newly issued edition of *A Climber's Guide to the High Sierra* and found that another pair of climbers had successfully climbed Darwin by this route, thus vindicating my hypothesis.

A third excursion of the summer of 1955 was made shortly before Bob went back to Colorado. Our destination was not the high Sierra itself, but a group of rocky peaks known as Sierra Buttes that rise above the forest near Downieville. The highest of them, the middle butte, has a four-wheel-drive road to its summit, but the south butte had no record of a climb and looked precipitous from all sides. We approached it from Sardine Lake, about three miles east of the buttes. To get to the south butte itself, we had to climb up a steep rocky trailless slope to a divide between two separate canyons and cross a boulder field for about a mile to the beginning of the northeast ridge leading up precipitous crags to the summit of the south butte. At the beginning of the ridge, we roped up and Bob climbed up and started to explore the lowermost crag. This turned out to require quite a lot of time, during which I was belaying him with the help of a spur of rock. When he was still busy with his exploration my eyes wandered over the face of the crag and received quite a shock. Spurting out from one of the small cracks in the face, was a rock fern that looked to me somewhat familiar. As I looked closer, my mind thought back to the summer of 1926 and a similar face in the Green Mountains of Vermont. I thought this surely must be the green spleenwort.

I couldn't help letting out a yell, at which Bob above me shouted, "Don't worry, I'm all right."

I yelled back, "That's great, but I just found a rare fern."

"The hell you have, you should be belaying me!" he shouted back.

I looked at the spur of rock over which the rope was belayed and verified that it was still there. I quickly grabbed a frond of the fern and while holding the belay in one hand, with the other I took out my wallet and put the fern in it. Soon after this operation was done, Bob called back asking me to climb up to him and we continued up the ridge, which turned out to be much easier than it looked from a distance, so that we reached the summit of the south butte via a new route well before noon. This combination of a splendid rock climb and a new discovery turned the day into one of the most rewarding of my career.

During the following week, I went to the herbarium and verified, first, that I had actually found the green spleenwort again 27 years after I had seen it in Vermont, and second, that there was no record of its occurrence in California or even in adjacent Oregon or Nevada, although it is common in Washington and British Columbia.[1]

In 1957, I acted at the suggestion of Norman Clyde, given to me when I was with him and Peter Raven on Coyote Ridge in 1950. This time we were joined by a young lady who was temporarily a close friend of Bob's. We had first contemplated another stab at the east face of Darwin but when Bob's friend saw it, she had cold feet. We then went up McGee Creek, which is just to the south of Convict Creek. This was to see whether, in 1950, Norman Clyde had been right when he said that the area was full of limestone. This was a correct observation, but all of the rock faces that needed a rope were so unsafe that we decided not to climb on them.

The next two climbs were done by three generations of Stebbinses. I had asked Bob and grandsons David and Dan, then aged 10 and eight, to go with me to our cabin at Wright's Lake west of Lake Tahoe. From the meadow just above our cabin we had a fine view of a peak about 8,500 feet that was not named on the map, but among Wright's Lake summer cabin owners was called "Pooch Peak," because it has a general resemblance to a dog with floppy ears lying down, feet foremost. This seemed like a good starter for boys of that age, so we hiked up a trail until we reached the crest of a ridge corresponding to the "hind end" of the dog and hiked up the ridge, which was open enough not to need a trail, until we reached the summit or front end of the "pooch." We were early enough to arrive there before the snow had melted on the northeast face, and so had a fairly fast but perfectly safe slide on our bottoms for about 1,000 feet. This brought us to the head of a small stream, which we followed to Tyler Lake and from there down a well-known fisherman's trail to Wright's Lake.

The next trip of note was another "four boys and men" Stebbins family trip with Bob, David, Dan, and me. Our objective was to climb together one of the Sierran Crest Peaks. We selected Red Slate Mountain, which dominates the headwaters of Convict Creek and McGee Creek about 20 miles south of the well-known Mammoth Ski Area. We approached it via Convict Creek and spent two nights camped at 10,000 feet above that Creek. The climb is not really a rock climb but a steep scramble that includes traversing the upper part of a large snow field. Bob led us across easily, and I was pleased to see that both boys, then 13 and 11, followed him without trouble or complaint. We

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1. Linnaeus first described *Asplenium trichomanes-ramosum* in 1753, followed by the synonymous name *Asplenium viride* Hudson in 1762. The Jepson Manual lists the distribution for the green spleenwort as "Sierra Co., e side of Sierra Buttes, to AK, e. N. Am., Eur., Asia," in J. C. Hickson, ed., *The Jepson Manual, Higher Plants of California* (Berkeley: University of California Press, 1993): 89. — VCH

got to the summit a little before noon, giving me time to perform a mountaineer ceremony by plucking a stem from each of two plants of the most beautiful alpine species of the highest Sierra, the sky pilot or *Polemonium eximium*. The Sierra Club tradition is that any mountaineer who has conquered a peak of 13,000 feet (about 4,000 meters) above sea level, is entitled to wear one stalk of this plant and display its clear blue flowers that match the clear sky above it. I had hardly finished the ceremony when thunder came rumbling to us from the peaks to the south, and we knew that we might be in trouble. We started down as quickly as we could without making dangerous missteps. We were well off the dangerous crest upon which lightning can strike without warning but still some distance from the campsite when the storm broke. As soon as we reached our camp, we gathered our supplies under our ponchos and waited it out. Like most midsummer thunderstorms in the Sierra, it was over in time for us to dry ourselves out in the late afternoon sun. The following day we returned home.

Two other trips taken with Bob and other family members and friends are memorable. After the Red Slate climb, family mountaineering continued with trips taken from Corvallis, Oregon, Bob's home. The first of these is significant because Bob's first wife, Lola, was with Barbara and me for the last time. In 1981, Barbara and I visited them in Corvallis, and we went together to the Cascade Mountains east of us. We first camped at a large meadow southeast of the south peak of the Three Sisters and enjoyed a walk to a small lake about three miles away. We then took a very rough road southwest and hiked up a gentle green meadow even closer to the south peak. There we found a fine campsite, and on the next day we went home via the foot of Diamond Peak, south of the Three Sisters and immediately above the pass through which the railroad and the principal highway cross the crest of the Cascades. At that time, my interest in sexuality and apomixis in *Antennaria* had been renewed, so that I was most happy to have Lola accompany me to visit and collect at a locality on the southwest side of Diamond Peak. This trip was the last one that Barbara and I shared with Lola and Bob before Lola's tragic death in an auto accident two months later.

Still another trip exemplifies the generosity and tolerance of my son Bob. This was again in the Oregon Cascades near the north end of Mount Jefferson and included a friend of his, Richard Grainger. This young man had gotten into trouble, been convicted of robbing a store, and was out of jail on parole. Bob had agreed to be the sponsor for his parole. After the trip, I had to agree that Richard was a really fine young man, well worth saving. The four or five days in the mountains were a pleasure from beginning to end. Again, I was looking for *Antennaria*, and Richard helped me a good deal with this little job. This trip in particular illustrates one of Bob's finest qualities, his desire to help others who are in trouble. I took other trips of a similar nature in Oregon with Bob, his second wife, Monine, and other friends.

About 1980, I climbed a 13,000-foot peak, Mount Morgan, with another group consisting of my colleague, the late Jim Boyd, four graduate students, and Claude Beguin, a botanist from Neuchâtel, Switzerland. The ascent of this mountain was no more than a scramble, but it did bring us well into the high-mountain altitudes that warranted decorating the neophytes with the sky pilot, *Polemonium eximium*. I decided to make a ceremony out of the affair and put the stalk of sky pilot in each of the climber's buttonholes and at the same time recite the words that were familiar to me from our graduation ceremonies:

"By the authority given me by the nymphs, gnomes, and leprechauns of these here mountains, I name you expert mountaineer of the Sierra Nevada of California."

Purposely, I left Professor Beguin to the end. While I was initiating the others, he was whispering frantically to them, "What is he saying?" Finally I got to him and

changed my language.

"Par l'authorité que m'a accorde les nymphes, gnomes et leprechauns de ces montagnes, je vous prononce montagnard extraordinaire de la Sierra Nevada de Californie et je vous donne tous les droits privilège qui vinnent de ce titre."

Claude was immensely pleased with this recognition of his language and asked me later, "How did you come to know all of the proper words that French officials use when bestowing a title upon somebody? Did you remember the words that they used when they awarded you your honorary degree at the University of Paris?"

I replied that I did. He wrote me later that he told this anecdote during a talk that he gave at his university at Neuchâtel and it went over very well.

The achievement of my final mountaineering ambition was to climb a 13,000-foot peak at the age of 80 in the summer of 1986. I selected Mount Dana at the head of Tioga Pass. Before joining the group as a whole, Barbara and I spent a preliminary weekend on Sonora Pass with Bob and Monine. I found that while my ability to cope with rough ground and steep slopes was much less in 1986 than in 1973, I could still handle the trailless terrain well enough that I was pretty sure that I could do the climb. I therefore went along with Bob and Monine and joined at the road head, the summit of Tioga Pass, the small group that I had invited, including grandson Dan and stepson Marc. The hike from Tioga Pass to the summit was little more than a steep walk. Although I made it without real difficulty, I still was so tired at the summit that I did not fully appreciate the champagne party that my friends had prepared for me. On the other hand, the descent was almost a disaster, because my knees gave out on me about midway down the mountain. Without Marc's strong arm, I would never had made it back down. This was one of the last mountaineering trips I took, although I did manage to climb the trail up Mount Lassen at 10,000 feet the following year.

Chapter 23
Leading the Charge for Plant Preservation

A set of episodes that took place between 1960 and my retirement in 1975 was connected with my election as president of the Botanical Society of America in 1961. In addition to the minimal presidential duties, the president must preside at the annual dinner that takes place during the year of his or her tenure, as well as the subsequent year when the successor presides and the past president delivers the evening lecture. As soon as I was elected, I realized that an unusual situation had arisen. Two successive presidents of the society had been elected from a single, not very large campus. At first, I decided to make an issue of this situation to show that in botany, our campus was much more noteworthy than might be expected from its relatively small size and orientation toward agriculture rather than basic science.

About a month after my election, things changed. Vernon I. Cheadle had been appointed Chancellor of the University of California campus at Santa Barbara. This made me change my mind with respect to introducing him as the principal speaker of the evening and making a wisecrack or two about our common origin from the Botany Department at Harvard.

However, when the diners had finished their meal and I had presented Vernon Cheadle with a few compliments and a rather bland introduction, he did, in fact, for me what I had planned to do for him. He started by repeating a completely mythological story that I had a few years earlier, in a fit of anger, thrown my desk typewriter out of the window. He followed up this story with reminiscences of seeing and hearing me when I was a graduate student at Harvard. He correctly related that I had been practicing my choral adventures, such as Beethoven's Ninth Symphony, while doing technical jobs in my cubbyhole of Professor Jeffrey's laboratory. He then launched into an impassioned plea for us not to be too much ashamed of ourselves and to repeat the word that botany has a significant role in modern society.

While he was talking, I suddenly decided to ask for a postlude, which would be what I might have given before being awed by Vernon's position as Chancellor. My mind wandered to one of my favorite operettas, Gilbert and Sullivan's *Iolanthe*, and its famous Lord Chancellor's song. Soon my wife, who was among the diners in the audience, noticed that my body was swaying from one side of my chair to the other and that my hands seemed to be pounding out an imaginary rhythm. In fact, she was right. Consequently, when Vernon had finished and received light but enthusiastic applause, I asked the diners if they would like to hear a sample of the singing to which Chancellor Cheadle had referred. The response to my request was warm and enthusiastic, so I produced what had come to me during the proceeding half hour:

He told you that one torrid fall,
I threw a typewriter into the hall,
He said I sang too loud and long,
It really was an innocent song,
He said I was beyond recall,
A botanist with no balance at all,
A kind of a nut I was the butt,
Of his wisecracks that amused you all,

But ... I took it as a compliment for
He's such a powerful Chancellor,
It really was a compliment for
He's such a powerful Chancellor.

My little ditty received such warm applause that I began to think about what I would do at New Haven in 1963, when my friend Art Galston would be the presiding officer and I the featured speaker. I had plenty of time to prepare this one, so that when the audience at the 1963 dinner was ready for me, I asked them if they would like to hear another of my parodies. They accepted warmly, so I sang for them a parody of the Major General's song from Gilbert and Sullivan's *Pirates of Penzance*, which I renamed for this occasion, "Song of the Molecular Botanist," which goes like this:

I am the very pattern of a botanist molecular,
I've information chemical and infra-organellular,
I know the structure ultra-fine of phage and coli chromosomes,
I've cracked the code from DNA to RNA and ribosomes.
I'm also well acquainted with reactions enzymatical,
I work out their kinetics using formulae quadratical,
From electronic resonance to physics of the solid state,
And all the clever methods by which cells of microbes conjugate.
In all these matters chemical and infra-organellular,
I am the very pattern of a botanist molecular.

I also know a lot about that stuff you folks call botany,
I know that weeds and trees have leaves, and fungi haven't got any,
I'm sure that horsetails, lycopods, and ferns
And so forth don't have seeds,
I heard today that 2, 4-D is ... rather good for killing weeds.
The latest dope about conduction vascular I'll tell you now,
I know that water flows up xylem fibers ... but I don't care how.
And — ugh, Taxonomy!
That I can't use a key to species doesn't bother me at all.
I just work out their matrices on my computer digital,
But yet in all things chemical and infra-organellular,
I am the very pattern of a botanist molecular!

These two performances of mine received such accolades that five years later, when I had joined several colleagues on the organizing committee of the XI International Botanical Congress at Seattle in 1969, they asked me to provide a short program of a lighter nature to be presented after the serious part of a dinner to be held on the final evening of the Congress. Again, I had plenty of time to prepare and reverted to my forte of parodies of well-known ballads or songs. Because the emblem of the Congress was the Douglas fir, chosen by the organizing committee in acknowledgment of the financial assistance given us by the Washington Timber Industry, my first parody was of the well-known French folk song "Alouette," with "*Pseudotsuga*," the scientific name of the Douglas fir, substituted for "alouette."

The second song had the tune of the famous Mexican ditty "La Cucuracha" but was about poison oak, the chorus being:

Oh don't scratch it, no don't scratch it,
They will only make it worse,

Try this ointment it may help you,
But if not, just sit and curse.

Finally, my other new endeavor I called "The Ballad of Pollution," a parody of "John Brown's Body," the tune of which was the later basis for "The Battle Hymn of the Republic."

Mary Ann McCarthy was a young and sweet co-ed.
She asked if she could study algae brown and green and red.
Her botany professor said "Yes, Mary, go ahead!"
But pollution had done them in.

CHORUS:
All that she could find was oil slicks,
All that she could find was oil slicks,
All that she could find was oil slicks,
'Cause pollution had done them in.

She put on rubber booties and went down to Skagit Bay,
She climbed on rocks and dug in mud throughout the live-long day. But algae,
brown and green and red,
They all had gone away,
'Cause pollution had done them in.
(CHORUS)

So Mary Ann decided she had something big to do.
She called on her professor and on all her boyfriends too.
She raised a mighty army and she shouts to me and you,
"Let's do pollution in!"

CHORUS:
Let's all put an end to oil slicks,
Let's all put an end to oil slicks,
Let's all put an end to oil slicks,
And do pollution in!

"The Ballad of Pollution" was not only the climax of my part of the evening but also the one that made echoes in the popular press. The morning newspaper, *The Seattle Times*, reported the activities of our Congress under the headline, "Botanist Upstages Scoop Jackson." They then reported the passionate talk that Washington's Senator Jackson had presented in the serious part of the dinner ceremony followed by my less serious part. They then interwove sentences from Jackson's oratory with my ballad in such a way that at least some readers would conclude that my words about pollution were more effective than those of the senator.

In 1968, I was awarded a research scholarship at the Center for Advanced Studies, nicknamed the "Think Tank" at Stanford. This institution attracts principally social scientists, but every year, one scholar in the biological sciences is invited with the hope that he or she will broaden the outlook of the social scientists. In my case I found so little in common with most of the other scholars that our interaction was not very great. For me, however, it was a fine opportunity to work undisturbed on my book *Flowering*

Plants: Evolution Above the Species Level.[1] During that year, 1968, my friend Jack Major and I, along with a graduate student, had an unusual opportunity to visit with one of Europe's most distinguished botanists, Armen Takhtajan, director of the Komarov Botanical Institute in Leningrad in the U.S.S.R. (now St. Petersburg, Russia). In the company of my colleague at Berkeley, Lincoln Constance, we picked up Armen and drove him first to Monterey and the 17-Mile Drive, and later to Big Sur Canyon State Park. We took him along a trail that traverses the side of Big Sur Canyon and passes by coast redwood trees at a height 200 to 300 feet above the bottom of the canyon, so that one has an unusual view of these trees from the middle of their trunks downward to the ground and up to the crown of foliage and cones. Dr. Takhtajan was very impressed with the visit and we had much to talk about in our mutual field of interest, the origin and early evolution of the angiosperms or flowering plants. On the return trip we crossed the crest of the Santa Lucia Mountains and made a short detour to show him the unusual conifer endemic to these mountains, the Santa Lucia fir *Abies bracteata.* This rather long trip allowed us to have a late supper at the nearest good restaurant in Salinas. Ordering our meal there was quite an experience for all of us, including the rather jovial and chatty waitress. The reason was that whenever she offered us a choice, such as soup or salad, the kind of dressing on the salad, the entrée, dessert, and coffee or tea, Jack and I made one choice and Armen made the opposite choice. Finally, the waitress looked at Armen and said, "You're an oddball, aren't you?"

Armen looked at us and said, "What is an oddball?" We explained with the result that all of us had a good laugh. I doubt that this eminent scientist would be treated with the same informality either in his own country or in normal circumstances in our country. Armen made remarks that indicated his pleasure at being introduced into such an informal facet of our culture. When we got back to Menlo Park late that night, Barbara greeted us and invited him to spend the night while Jack and the student stayed elsewhere.

Armen's first comment was, "What has happened to my miserable country while I was away?"

Barbara had to explain that Russian power had been exerted and that Russian tanks on this day in 1968 were rumbling through the streets of Prague.

At this same time, I began my conservation activities with the California Native Plant Society (CNPS). In 1966, I heard about the recent formation of this society from a colleague in the Berkeley Department of Chemistry. Apparently he and a number of other Berkeley faculty members had been disturbed by the likelihood that the arboretum of native California woody plants long established in Tilden Park in the East Bay would be dismantled and that James Roof, a fine horticulturist and avid explorer of our native flora, would be dismissed from his position. This group joined with other plant lovers of Berkeley and succeeded in their campaign to save both the arboretum and Jim Roof. They enjoyed this so much that they thought of an alternative to disbanding after the success of their campaign. They therefore formed the nucleus of the California Native Plant Society and spread the word throughout the state asking other enthusiasts for conservation of plants by any means whatsoever.

I was immediately taken up with this idea and started a chapter of the Society in the Sacramento Valley, particularly Sacramento and Davis. The following year, the group discovered that they had become somewhat overenthusiastic in their organization. In particular, they had hired a secretary and rented a room in a Berkeley store for monthly evening meetings and in this way had incurred a debt they could not pay. I had been

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1. G. Ledyard Stebbins, *Flowering Plants: Evolution Above the Species Level* (Cambridge, Massachusetts: Belknap Press, 1974). — VBS

chairman of the Davis chapter for about six months during which I started a program of regular field trips. At the same time Professor Watson M. Laetsch, a botanist of UC–Berkeley who had been elected president, was appointed by the university to be director of the Museum of Physical Sciences established by the Atomic Energy Research Group. He therefore resigned as president of our society, and I was asked to take his place. This included chiefly a missionary series of visits to outlying groups in order to persuade them to establish separate chapters, thereby increasing our membership. At the same time, those of us at that meeting discussed constantly, almost in desperation, our financial plight and wondered how we could pay our debts.

Fortunately, four stalwart participants of the previous Tilden Park Organization, Joyce Burr, Jenny Fleming, Susan Fruge, and Lenore Strohmeier, pointed out that Jim Roof, now reinstated at Tilden Park, had extra nursery stock of native plants to which the others said they could contribute enough to make possible a native plant sale to prospective gardeners. With some apprehension we announced this sale to be held under the auspices of the Tilden Park Arboretum. The result was spectacular. It had been advertised as taking place from 9:00 until noon on a Saturday morning. However, by 11:00, nearly all of our stock of plants was exhausted and we had netted $4,000. This success put the fledgling society on a firm basis from which we were able to build.

My job as missionary was delightful, as through it I became acquainted with a number of native plant lovers throughout the state. One of my closest friends who dates from this time is Don Smith from Placerville, a wholesale lumberman now retired. We joined in a number of excursions throughout the northern Sierra. He showed me a beautiful meadow situated northeast of Placerville at an altitude of 4,000 feet. The meadow itself was noteworthy for possessing three species rare in the area, Bolander's mock dandelion, *Phalacroseris bolanderi*; the white beaksedge or white beakrush, *Rhynchospora alba*; and the round-leaved sundew, *Drosera rotundifolia*. In addition, the borders of the swampy meadow contained two species that are near the southern limit of their distribution. After we had visited this site two or three times, Don discovered that he could buy it for a small price and convert it to our Society's own reserve.

Four different examples of conservation illustrate the policies that we adopted to get results in an efficient way. The first of these was called to our attention by the director of the Stanford Marine Laboratory of Pacific Grove, who owned a home in the Del Monte Forest between Pacific Grove and Carmel. This area contains a very unusual plant association due to the fact that it is a raised beach underlain by a fossil soil that is two million years or more old. I had already nicknamed the area "Evolution Hill" because of several species in it that provide textbook examples of how plants evolved. During the 1940s, I had approached the owner and director of the Del Monte Forest and pled with him to preserve this area. He replied that he too was very fond of the area, which was near his own home and provided fine opportunities for hiking and horseback riding in a little-visited area. However, he was getting along in years, he said, and could not tie his successors down to any arrangement.

When he died, the man who was chosen to succeed him was a former company manager of the Corning Glassworks who felt that the best use for "Evolution Hill" was to quarry it to recover its fine grade of sand useful in making glass. Because of the new owner's decision, all of the property owners who had built or bought expensive luxury homes in the area were faced with the prospect of the clanging noise of a quarry and would lose the area that was one of their favorite places for the enjoyment of solitude.

As soon as I heard about this danger, I scheduled a meeting of the California Native Plant Society. When we asked the administrators in charge of the 17-Mile Drive area if we could stage a trip that would give the people a chance to look at it and explain that it would be a site visit rather than a protest march, they were most sympathetic with us and allowed us to go ahead. We assembled more than 100 people, including local property owners and members of our society who collaborated to ask

for a hearing on the subject and protested to the superintendents of Monterey County. The use of this area was previously considered to be purely for recreation, but now it was to be subverted for commercial use. The result of our activity was that, at present, much of the area is designated and advertised as the S. F. B. Morse Botanical Reserve. This success showed us how valuable it is to join with other people who have similar interests and more influence.

My second example concerns a swamp in the Sacramento Valley near the town of Colusa. The plant species that it preserves is the California rose mallow[2] that was formerly common in the Delta area but had been recently almost wiped out in that area by agricultural activity. I visited the Colusa swamp and found that this area was undisturbed by agriculture and in it the California rose mallow was abundant. Because it was owned by a duck hunting club whose members lived in San Francisco, I went first to their resident warden and asked him about the rose mallow. When he realized what I was talking about, his face lit up and he explained that to them it was of great value because its seeds ripened at about the time the southward migration of water fowl takes place and that their abundance attracts large numbers of ducks at just the time the hunters arrive. I didn't need to go further. I learned from this experience that the more that can be found out about a rare plant that one wishes to preserve, the more likely one is to find additional reasons for preserving it.

We found a similar community of interest with respect to another area that we wished to preserve in Tiburon, a suburb of San Francisco. The principal rare species was the black jewelflower *Streptanthus niger*.[3] Although it once existed over all parts of the peninsula underlain by serpentine rock, it survived only in the area surrounding the old Catholic church. When the church's congregation moved to a larger building away from the serpentine area, we were afraid that further suburbanization would render the black jewelflower extinct. However, some members of our Marin County chapter discovered that many Catholic residents of the area felt that the wooden church building was a relic that should be preserved. We therefore were able to join with them and raise enough money, both from our own members and others, to buy and preserve the land encompassing the church and the surrounding grassy area containing the jewelflower. A similar community of interest enabled us to preserve another area in Tiburon known as Ring Mountain that contains the Tiburon mariposa lily.[4]

My final example is a vernal pool in Lake County known as Boggs Lake. One day in midsummer, the secretary of the CNPS telephoned to tell me that the County Board of Supervisors of Lake County was holding a hearing to decide whether or not a real estate

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2. The Jepson Manual lists the rose mallow in California as *Hibiscus lasiocarpos* Cav., 1787. The Californian plants had been segregated by Kellogg in 1873 as *Hibiscus californicus*. L. H. Bailey returned these to *Hibiscus lasiocarpos* in 1915. The Jepson Manual synonymized *californicus* to *Hibiscus lasiocarpos*, noting it as "RARE in CA. Wet banks, marshes." J. C. Hickson, ed., *The Jepson Manual, Higher Plants of California* (Berkeley: University of California Press, 1993): 750. — VCH

3. In the mustard family Brassicaceae, the black or Tiburon jewelweed *Streptanthus niger* Greene, *Bull. Torrey Bot. Club* 13 (1886): 141, was later transferred by Greene to *Euclisia nigra*, *Leafl. Bot. Observ. Crit.* 1 (1904): 83. *Streptanthus niger* is listed in The Jepson Manual as "RARE. Serpentine outcrops in grassland." J. C. Hickson, ed., *The Jepson Manual, Higher Plants of California* (Berkeley: University of California Press, 1993): 443. — VCH

4. The Tiburon mariposa lily was later distinguished as *Calochortus tiburonensis* A. J. Hill, *Madroño* 22 (1973): 100–104. The Jepson Manual lists it as "THREATENED CA. Serpentine grassland…Ring Mtn., Marin Co." J. C. Hickson, ed., *The Jepson Manual, Higher Plants of California* (Berkeley: University of California Press, 1993): 1188. — VCH

company located in Oakland could obtain a permit to develop Boggs Lake and its surroundings for recreational purposes. I immediately told her that I would be there, as I was and still am particularly fond of the area. Furthermore, I took pains to visit the area before going to Lakeport for the hearing because I suspected that I could tell people that the promoters had probably overemphasized its recreational possibilities. I turned out to be correct. When their representative spoke, it became clear that they had not visited the area on the ground, but had been captivated by its appearance in spring when it was a limpid blue lake about one-half mile in diameter surrounded by what from the air appeared to be a splendid forest of Ponderosa pine.[5] I discovered that the "lake" as viewed from the ground in August is a mudhole, completely dry around its margins with a few tule reeds in its center. Furthermore, the pine forest consists of trees hardly more than a foot in diameter and so densely spaced together that many of them would need to be cut down for each building that could be built. When I explained all this to the supervisors, others who knew the area raised a great question as to whether fresh water could be found in the near vicinity to supply a resort community. The evidence presented, which was new to development company's representative, was so convincing that he gave up his request to develop the property and gave us the chance to submit it for preservation of its rare plant species by the Nature Conservancy.

Such experiences have been duplicated in other areas so that our knowledge has been of great use in preserving particularly the less well known of California's treasure trove of native habitats.

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5. The Jepson Manual lists the Pacific Ponderosa pine as *Pinus ponderosa* Laws. J. C. Hickson, ed., *The Jepson Manual, Higher Plants of California* (Berkeley: University of California Press, 1993): 120. — VCH

Chapter 24
A New Direction in Research Leads to Edinburgh, Paris, and Stockholm

By 1957, I had decided that I could have a more interesting and valuable research career by shifting from grass breeding to the general problem of the pathway from gene expression to visible characters in whatever plant group seemed to offer the best possibility.

I had two reasons for making such a shift. First, I realized that the most important discoveries and theories for evolutionists to consider at that time had to do with evolution above the species level. Second, problems of plant morphology required thinking in terms of changes in shape and form, a type of problem that had always attracted me. As a child, I often became absorbed in picture puzzles and was somewhat of an expert. Still another reason was that the immediate task of plant evolutionists was to understand fully the meaning of general theories of evolution, the then newly discovered importance of nucleic acids, both DNA and RNA, and how they affect all thinking about problems in biology.

In my preliminary research in this field I persuaded a graduate student, Bert Huether, to attempt a selection experiment on a small California annual, *Linanthus androsaceus*.[1] I had observed several populations of this species in the field and found that all of them contained a small percentage of plants having more than the usual five petals or corolla lobes. He found that starting with these abnormal plants he could, in a few generations, produce progeny having as many as 13 corolla lobes or as few as four. However, these plants were very weak and unsuitable for further experimentation.

While Bert Huether was doing his research on *Linanthus*, I decided that I would need a broader perspective on plant development before using comparative development as a tool for understanding evolutionary processes. I therefore applied for and had the unusual distinction of receiving a second Guggenheim Fellowship in order to spend several weeks in 1961 in three different research centers: the University of Edinburgh, Scotland; the laboratory of my former host, Marcel Guinochet, at the Paris suburb of Orly; and Stockholm. At Edinburgh, Professor Robert Brown appeared to be doing interesting work on the genetic basis of plant form, while on the animal side, C. H. Waddington was a leading developmental geneticist. The value of Guinochet and Paris was chiefly in connection with the phytotron, an apparatus of successive rooms creating a series of different but constant environments, at the neighboring suburb of Gif-sur-Yvette. At Stockholm, my friend Åke Gustafsson had assembled an extensive collection of artificially produced mutant strains of barley that seemed to offer better possibilities than any other plant species.

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1. Bentham established the genus *Linanthus* Benth. in 1833 within the Polemoniaceae. Greene recognized the species *Linanthus androsaceus* in 1892. In California, The Jepson Manual places it in "Open or shaded areas in woodlands, chaparral... . Many variants often placed here are synonyms of *L. parviflorus*" [(Benth.) Greene]. J. C. Hickson, ed., *The Jepson Manual, Higher Plants of California* (Berkeley: University of California Press, 1993): 842. — VCH

When I got to Edinburgh and discussed developmental problems with Professor Brown, I realized that our hypotheses were not compatible with each other and that his experiments had little to offer me. I did, however get some good ideas about the relation between orientation of mitotic spindles and form from a graduate student, Robert Lyndon, who was beginning research in this field and during the following years obtained a lot of valuable data. As for Waddington, his experiments with *Drosophila* fruitflies were too far away from my experience with plants to be of direct value. So too, his theories were based upon analogies that could not be applied to plants and so also had little direct value to me. My experience at Edinburgh taught me how little was known that could be used to understand better the relationship between genes and characters in higher plants.

During my stay in Britain, I visited several laboratories in which research was being done that was important to me in relation to either plant genetics, chromosomes or the rapidly expanding field of cellular ultrastructure, and the excellent ecological investigations by John Harper at Bangor, Wales. On a visit to Oxford, I distinguished myself with one of the most glaring faux pas that I ever uttered. I had just gone to Oxford from Leeds, where Professor Irene Manton had discussed with me her former work on chromosomes of ferns and more particularly her current work, which was attracting a great deal of attention on the ultrastructure of plant cells. My host at Oxford invited me to lunch at an elegant garden party, which was full of good conversation. In the middle of the party, I commented on the work of Manton that I had just seen. One of the faculty wives then asked me, "Who is Irene Manton?"[2]

My host broke in and said contemptuously, "She is one of those awkward Newnham women." Newnham is the women's college associated with Cambridge University and not highly regarded by Cambridge dons attached to men's colleges.

This raised my hackles to the extent that I came out with this blockbuster: "I have been visiting a whole series of excellent botanical laboratories and the only one in which I have seen good work being done by a botanist who is over 50 is that of Irene Manton." The implication was clear, as my host was over 50 and not doing anything of importance.

In Paris, my most valuable help was provided by the younger botanists working in the phytotron at Gif-sur-Yvette. I was persuaded that constant temperature chambers would be essential for my future research. Paris was also a place to relax with Barbara and to enjoy entertainment of various sorts. The one we both remembered most vividly was engineered by Professor Pierre Chouard, one of my companions in the International Union of Biological Sciences. Through him we got an invitation to dinner from Madame Roger Vilmorin, whose husband was a descendant of the horticulturist family appointed by Louis XVI to improve the gardens at Versailles. She treated us to a dinner of filet mignon plus the latest new varieties of asparagus and other delectable vegetables, washed down by an elegant wine of a vintage I do not recall. Because she was English, she and Barbara had an excellent and memorable conversation.

A spin-off from this conversation with Chouard and Vilmorin was probably responsible for my receiving an honorary doctorate from the University of Paris a few years later. Of the visit I took in order to receive this degree, I have many delectable memories, not the least of which was a conversation across the ocean. I had been lodged by the Awards Committee in the Hotel Louvre and was just beginning to gain consciousness after a deep sleep in its soft bed when the telephone rang. I picked up the receiver

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2. Irene Manton (1904–1988) was one of the most distinguished botanists of the 20th century. She was an expert on algae and one of the pioneers in electron microscopy and other microscopical techniques. She was made a Fellow of the Royal Society in 1961. — VBS

and started mumbling something while I heard similar mumbling from the other end. In a mixture of French and English finally the exclamation, "Oh honey!" came out loud and clear. We had not been able to finance Barbara's trip to Paris, which was some time after our 1961 visit, but our warm greetings made up a little of the gap in failing to have her with me.

Returning to 1961, Barbara and I went from Paris to Stockholm, where Åke Gustafsson had found a most comfortable hotel for our two-month stay. I immediately started looking through the morphological mutants that he had available for me, and found one in which the epidermal complexes lacked subsidiary cells. As I had been able to induce this condition by environmental manipulation in barley, this appeared to me to be very promising material. Consequently, I took back to Davis seeds of this mutant known as "Bright Green" and did some preliminary experiments on the assumption that it was a recessive mutant, a fact already known, and that the recessive homozygote lacked the ability to synthesize some enzyme or amino acid. Because all attempts to proceed further produced only negative effects, I did not continue research on it. Later on, when I had tried several other genotypes with little success, I decided from this research that the failure of gene action in the recessive mutant was more likely due to an upset in the complicated developmental process that generates subsidiaries in the normal leaf. Perhaps a distinction between biochemical mutations that do not produce morphological change differ from those that do, in that their effect is confined to a single biochemical synthesis, whereas morphological changes involve alteration of a pathway that involves two or more syntheses that bear a particular timing in relationship to each other.

On my way back to Davis from Stockholm, I visited with my friend Wacek Gajewski in Warsaw, Poland. Unfortunately, the Polish authorities provided a visa for me for the sake of science but not for what was to them extra baggage such as a spouse, therefore Barbara went home separately. Since Wacek had turned his attention from higher plants to fungi, I could only admire what appeared to be very interesting and modern scientific research. We did, however, end my visit with a most rewarding trip to the Tatra Mountains of southern Poland and neighboring Czechoslovakia. Its high point was a glorious trip to a mountain situated on the divide between the two countries. While sitting on a mountaintop and having lunch with Wacek, I reached my Waterloo in writing down the names of neighboring summits, which has been for many years my custom. Looking at a map that Wacek had, I saw that the name of the mountain immediately to the south in Slovakia was Strbski Szczyp. I asked Wacek to pronounce this for me and he replied, "I can't. You see, it is Slovokian and, as a Pole, I don't know their language."

After reaching home and renewing the research of my students and me, I decided that from then on we would concentrate on mutants of barley, exploiting avenues that had opened up both during the trip and previously. Cultivated barley seemed to be particularly appropriate, because it is normally self-fertilizing and therefore individual lines remain constant from one generation to another, though outcrossing is easily performed if necessary. Two types of problems attracted me most. One of these is the pattern of cellular differentiation in the leaf epidermis. With respect to this problem, I could not find any mutations that I was able to analyze. The developmental nature of the absence of subsidiary cells in the "Bright Green" mutant was not open to analysis by means of any method that I could think of. I therefore turned to the hooded mutant. This turned out to be most interesting but quite complex. In order to solve the difficult problems involved, I realized that a multidisciplinary approach would be the only one that would be rewarding. Nevertheless, I had partial help from two graduate students. One of them was Ezra Yagil from Israel, with whom I collaborated to show that the most

critical effect of the hooded gene complex was increasing the frequency of mitosis at a particular early stage of development when this increase interfered with the normal elongation of cells necessary to produce the long awn on the floret in a normal barley plant. Instead, a much shorter awn was produced and between this reduced awn and the enclosed grain itself is a highly complex structure. The second graduate student, Vimal Gupta, showed that at the particular stage when the frequency of mitosis increased, the developing barley spikelet was exposed to a higher concentration of a peroxidase enzyme that may be associated with the change in mitotic frequency. The probability that this was true was increased by the fact that three different inhibitors of peroxidase activity, each of them applied in a different experiment, produced a much weakened expression of the hooded character. To find out the nature of this correlation would require the culture of living reproductive apices, which we were not able to do. This caused both graduate students and me to abandon the project.

During the years between 1950 and 1970, a number of events took place in addition to my divorce and new marriage, my teaching activity, and the end of my chairmanship of the department at UC–Davis. I appointed as my temporary successor a visitor from Australia, Alex S. Fraser, but this proved to be the biggest mistake I ever made in my career. I was attracted to him because of his grasp of genetics as a whole and his ability to communicate. However, his research on *Drosophila* was unattractive to Mel Green, and he was probably on the wrong track. After a feud that lasted for two years, the department replaced Fraser with a local staff member, Robert Allard, who transferred to our department from Agronomy. Fraser moved to the Animal Science Department and turned over to me the task of teaching the course for nonmajors on heredity and evolution. This was the substitute for the Berkeley course on evolution that I had abandoned. After a few years, Fraser left our campus for the Department of Biology at the University of Cincinnati.

After Fraser's departure, the chairmanship was held alternately by Bob Allard and Dick Snow. As for my own activity, my associations with the Integrated Studies group led to more committee work and enough regard from members that I became president of the All Campus Academic Senate, a position that I held during 1967.

This was a series of critical years for university campuses throughout the country and was particularly acute on the Berkeley and Santa Barbara campuses of our university system as well as San Francisco State University. Our task in Davis was to keep faculty-student relationships on as even a keel as possible. We were relatively successful in this regard for two reasons. First, the disturbing influence of an urban group of protesters that in Berkeley fueled the fire of this discontent existed near us only in Sacramento and affected chiefly Sacramento State University. The second was the constant vigilance of our Chancellor and Mrs. Emil Mrak. During the most critical years, they asked to be invited for dinner at either a dormitory, fraternity, or sorority once every week so that they could feel the pulse of student content or discontent.

Chapter 25
Hypotheses About Evolution Above the Species Level

My second most important book, *Flowering Plants: Evolution Above the Species Level*, remains the most controversial book that I have published. Even now, a large proportion of botanists who are interested in plant evolution do not accept what I wrote, even though I do not know of any direct criticism of the book that appears to be valid.

The book was written between 1968 and 1970, 10 years after I first had the idea of writing it. This idea developed from my invitation in 1958 to deliver the Prather Lectures at Harvard. I found that most of my audience, who were interested in evolution, appeared to be sympathetic with what I was saying but not so the botanists such as Irving W. Bailey. In fact, it was this difficulty of gaining acceptance from them that caused me to wait 10 years in hopes that further facts would be obtained that would make it easier to convey my points. This proved to be true to some extent but not enough to cause the botanists at Harvard who produced the most widely read books and papers to indicate their acceptance. Besides Bailey, I can mention Arthur Cronquist, at the New York Botanical Garden, with whom I always had a pleasant relationship because of his genial character and willingness to listen, but against whom I had so many contrary opinions that I often thought of myself as a "Cronquistador."

Two Europeans who did not agree with me were Fritz Ehrendorfer at the Universität Wien in Vienna and Armen L. Takhtajan, director of the Komarov Botanical Institute in Leningrad (now St. Petersburg). In Britain, relatively little attention was paid to *Flowering Plants* by E. H. Corner and others. With respect to all of them, the basic difference was whether one pays maximum attention to taxonomy or to ecology and genetics. The pure taxonomist is likely to accept the classic hypothesis of J. C. Willis,[1] who believed that the center of origin of a group is the area that at present contains the largest number of species belonging to that group, whereas the ecological outlook examines the adaptational complex of primitive groups and asks the question: What mutational changes would have been necessary to convert plants belonging to an older taxon to those having characteristics of a newer one? For instance, the hypothesis of Art Cronquist was that, since the largest number of angiosperm families occur in the tropics and are most highly developed in moist regions, the angiosperms must have originated in moist tropical habitats. By contrast, the ecological point of view emphasizes the fact that the principal differences between angiosperms and all other modern seed plants are

1. John Christopher Willis (1868–1958) was the British proponent of the "age and area" theory of phytogeography. First formulated in 1915, the theory proposed that the range of a given taxon depends on the age of the taxon. The range, in his view, therefore was an indication of the age of the taxon. Among other titles, Willis may be remembered for his publication of *A Dictionary of the Flowering Plants and Ferns* (Cambridge, United Kingdom: University Press, 1897). The book was reprinted in eight further editions through 1988. Willis was the director of the Royal Botanic Gardens, Ceylon (1896–1911), then director of the Botanical Garden, Rio de Janeiro in Brazil (1912–1915), later working at Cambridge; and F. A. Stafleu and R. S. Cowan, *Taxonomic Literature 2*, volume VII, *Regnum Vegetabile* 116 (1988): 331. — VCH, VBS

the reduction in length of the gametophytic stage of the plant life cycle, the rapidity of pollination provided by the style and stigma, and the direct development of the embryo (as contrasted to the indirect development in conifers as a proembryo is intercalated between the dividing zygote and the mature embryo). Because all these differences are associated with the more rapid completion of the reproductive cycle, the ecological hypothesis states that, to bring all of these changes about, a maximal advantage would have to be gained by speeding up development both before and after fertilization.

I have been greatly heartened by several recent publications, first by J. A. Doyle and M. J. Donaghue in *Paleobiology* in 1993[2] and more recently by Peter Crane, Else Marie Friis, and Klaus Pedersen in *Nature* of March 1995.[3] These authors espouse the hypothesis that ecological adaptation played a large role in the origin of angiosperms although they do not specify a particular scenario. To expand on my ecological theory, pollen evidence suggests the presence of angiosperms first at low paleolatitudes (Crane and Lidgard).[4] During the lowermost part of the Cretaceous period, which most paleobotanists agree is the time that angiosperms originated and spread quickly, there was a warm and moist climate, but this may have been followed by a seasonal monsoon-type climate in which a moist warm period was sandwiched between two cooler dry periods, at least in some regions of low and middle latitudes.

Consequently, the first step in looking for a favorable part of the world for the origin of angiosperms is to look for a region where a monsoon climate is adjacent to an equable tropical climate. Particularly favorable has been such a region in which a great deal of uplift and mountain building has taken place so that cool tropical mountain climates are often adjacent to much warmer ones.

Such regions of juxtaposition are widely scattered and separated from each other by regions that are either flat with little chance of developing montane habitats or have a different climatic cycle. In the New World, examples include Mexico and northwestern Argentina, and in the Old World there are such small regions in and around Africa, but an extraordinarily great concentration of them exists in Southeast Asia, the adjacent East Indies, and Australasia.

I should like to propose that the climatic conditions that promoted the origin of the earliest angiosperms from their possible common ancestor with the Gnetales and various extinct fossil groups were similar to those that presently prevail in northeastern Australia, New Guinea, and the mountains of Malaysia and southern China. In these regions, equable and moist climates like those prevalent in Indonesia pass either gradually or abruptly into climates of the monsoon type with wet, warm summers and dry, cool winters. In particular, regions like southwestern China and adjacent northern Vietnam, Thailand, and Burma (now Myanmar) contain steep-sloped mountain ranges that place the equatorial and monsoon climates close to each other, and the rugged topography makes possible the existence, side by side, of very different adaptive conditions.

Indirect evidence favoring a southeastern Asian center of origin for the most primitive angiosperms includes the present distribution of the majority of the small families

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2. Also at UC–Davis with Stebbins, James A. Doyle, and Michael J. Donoghue, University of Arizona, published "Phylogenies and angiosperm diversification," *Paleobiology* 19 (April 1993): 141–167. — VCH

3. P. R. Crane, E. M. Friis, and K. R. Pedersen. "The origin and early diversification of angiosperms," *Nature* 374 (1995): 27–33. — VCH

4. Scott Ligard published two relevant papers with Peter R. Crane in 1988 and 1989, respectively: "Quantitative analyses of the early angiosperm radiation," *Nature* 331: 344–346; and "Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity," *Science* 246: 675–678. — VCH

that in many phyletic treatments of the class (such as the treatment of Cronquist) are placed in the Magnoliidae, the most primitive superorder. One can mention here nine genera (out of 12) in the family Magnoliaceae as well as other families (10 placed by Cronquist in his subclass Magnoliidae)[5] that are represented either in entirety or in part by genera or species in this region (southern China or Asia south to northeastern Australia).

Because the angiosperms originated not later than the early Cretaceous, we must consider the position of the continents in the Jurassic and early Cretaceous periods. The volume by Charles S. Hutchison on the *Geological Evolution of South East Asia* (1989) states that during this period the ancient continent of Gondwana was continuing to break up, and various plates of the earth's crust were moving either through or near this southeastern region. This movement of tectonic plates also favors the idea of southeastern Asia and adjacent islands as the place of angiosperm origin. Movement of plates involves an increase in tectonic activity, including changes in climate at any one fixed part of a region, plus vulcanism that opens up new territory after the volcanoes have subsided and the soils are receptive to plants.

That is the most probable environmental scenario under which the flowering plants evolved. The possible nature of the earliest flowering plants and their relationship to the nearest gymnosperms, the seed plants that do not bear "typical" flowers, was a problem considered by Darwin in his *Origin of Species*.[6] Thereafter, he wrote that the origin of flowering plants is "an abominable mystery."[7] In generating my theory, which I admit is somewhat speculative, I paid principal attention to the anatomy and development both of the pollen-bearing structures or microsporophylls and of the ovules and carpels from which seeds arise.

With respect to the microsporophylls, I have focused on the variation in number of the individual pollen-bearing stamens and filaments, which range from only one per flower in some species to several hundred in some large flowers such as peonies or as in the strange flowers borne near the roots of some species of the tropical plant family Lecythidaceae. In at least some of these flowers, clusters containing many stamens are arranged in a whorl or spiral that resembles the whorled or spiral arrangement (phyllotaxy) of individual petals and sepals. The mechanical reasons for possession of a particular kind of phyllotaxy, such as whorls of three or five, are somewhat uncertain. Nevertheless, the fact that when any kind of phyllotaxy can be recognized in a flower that contains a large number of stamens — let us say 40 or more — the individual stamens are not arranged in a recognizable sequence of phyllotaxy, but clusters of stamens are so arranged.

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5. Arthur Cronquist (1981) lists 10 families for his subclass Magnoliidae: Winteraceae, Degeneriaceae, Himantandraceae, Eupomatiaceae, Austrobaileyaceae, Magnoliaceae, Lactoridaceae, Annonaceae, Myristicaceae, and Canellaceae. Pg. xiii in *An Integrated System of Classification of Flowering Plants* (New York: Columbia University Press). These 10 families also appear in his 1988 book, *The Evolution and Classification of Flowering Plants* (New York: The New York Botanical Garden): 503. Similarly in 2005, the Angiosperm Phylogeny Website (http://www.mobot.org/MOBOT/Research/APweb/welcome.html) lists six of these: Annonaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, and Myristicaceae. — VCH

6. Charles Darwin, *On the Origin of Species* (London: John Murray, 1859). — VBS

7. The rapid diversification of the angiosperms during the Tertiary was first termed "an abominable mystery" by Charles Darwin in a letter to J. D. Hooker (22 July 1879). Cf. F. Darwin and A. C. Seward, eds., Volume 2, *More Letters of Charles Darwin* (London: John Murray, 1903). Cf. also T. J. Davies, T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis, and V. Savolainen, "Darwin's abominable mystery: insights from a supertree of the angiosperms." *Proc. Natl. Acad. Sci. U.S.A.* 101 (2004): 1904. — VCH

With respect to the female part of the flower, or in the female flowers in species in which they are separate from the male flowers (or in the catkin and acorn of an oak), the female flower is often reduced to a single unit surrounded either by a whorl of sepals or by a subtending leaflike bract. The mature ovule-bearing structure itself may be a fruit that contains a single seed. In many, and probably in the original flowering plants, the ovule that becomes the seed has two coverings, or integuments. In all nonflowering seed plants, or gymnosperms, only one integument is present, surrounding the food material called endosperm and the embryo itself. A problem that is highly relevant to the ancestry of flowering plants is the nature of the outer integument. In most flowering plants, the two integuments are essentially alike but in some angiosperms, including species that belong to families considered relatively primitive, the outer integument is visibly different from the inner integument, both in its tissue structure and in the location of the opening or micropyle through which the pollen tube must pass. Because of these differences between integuments in some groups, I regard the outer integument as not directly homologous with the inner integument of the same ovule, but rather as representing a whorl of organs that was between the inner integument and the stamens but is now very much reduced. In some forms that may have been ancestral to the flowering plants, there was an intermediate, cuplike structure that has been called a cupule. Cupules containing several ovules are known in a fossil form that preceded flowering plants in the biological record, and other cupules that possessed a single ovule were present in the Corystospermataceae, which existed several million years before the time when flowering plant pollen or other fossils are known to have existed. This group was contemporaneous with the Ice Age known as the Permian glaciation. Thus, I suggest these as being related to the flowering plant ancestral types.

My opinion differs from that of contemporary plant evolutionists such as K. C. Nixon, P. R. Crane, K. R. Pedersen, and E. M. Friis in that I believe that the immediate ancestor to the flowering plants must have possessed a series of organs that did not have counterparts among other gymnosperms such as conifers, cycads, and the genus *Ginkgo*. Recently, evidence obtained by Charles Gasser, a biochemist at the University of California, Davis, showed that one mutant his group analyzed in explaining the development of the angiosperm or flowering plant ovule brought about a reversion of tissues of ovules so that some cells or filaments were more characteristic of stamen filaments. Another mutant known as *bel1* transforms the outer integument into a somewhat carpellike structure that has radial rather than bilateral symmetry, but this mutation has no effect on either the carpels (which are preserved in their entirety) or on the inner integument. These studies support the idea that the outer integument originally arose from modifications of some kind of organs surrounding the inner integument. This information, plus other facts that are well covered in articles by K. C. Nixon et al. (1994) and J. A. Doyle (1994),[8] has shown satisfactorily to me and others that all flowering plants have a common origin and that another, separate common origin can be ascribed to the group known as the Gnetales.

This latter group deserves special attention. The Gnetales consists of only three genera, which in their outer form and in their ecological habitat are as different from each other as are some of the most extreme members of the angiosperm phylum, but these genera are held together by similarities in the development of their reproductive

8. The following two papers may be relevant, among others by these authors in 1994. K. C. Nixon, W. L. Crepet, D. Stevenson, and E. M. Friis, "A reevaluation of seed plant phylogeny," *Ann. Missouri Bot. Gard.* 81 (1994): 484–533. J. A. Doyle, "Origin of the angiosperm flower: a phylogenetic perspective," *Pl. Syst. Evol., Suppl.* 8 (1994): 7–29. — VCH

structures and by similarities in their pollen. The best known of the three is *Ephedra*, from which the drug ephedrine was originally obtained and which lives in cool or cold deserts or steppes in both temperate Asia and in temperate North America. It is a much-branched shrub that consists almost entirely of woody stems only slightly covered by thin, scaly, nongreen leaves. The second genus, *Gnetum*, consists primarily of species of woody vines or "lianas" having broad green leaves like those of many flowering plants, and is confined to low, moist, pantropical forests. The third genus, *Welwitschia*, is even more extraordinary. It is confined to one of the world's driest deserts — that of Namibia in southwest Africa. A single plant consists first of a huge root, the size of about 100 carrots, that supports two huge ribbonlike leaves that spread across the desert for several feet. Between the leaves are the reproductive organs borne close to the ground on very short stems that, in their structure and development, resemble those of *Gnetum* and *Ephedra.*

The primary point I wish to make about the Gnetales is that, although they are almost certainly a sister group to the flowering plants, the evolutionary lines leading to these two groups must have separated from each other more than 100 or even 200 million years ago when both groups were very different from their present condition with respect to the genera and species that they contained. The ancestral links between genera of the Gnetales must have consisted of adaptive systems that may have been entirely different from those of the modern genera and about the nature of which we have no clue. The same uncertainty is equally true for possible links between Gnetales and flowering plants or even for links between the groups of flowering plant families themselves.

As an example of the latter problem, one of the genera regarded as most primitive among flowering plants (i.e., *Drimys* in the Winteraceae) contains species in Australia, New Zealand, and South America that must have been separated from each other before the Tertiary period. The chromosome numbers found among the Winteraceae are $2n = 26$, $2n = 28$, and $2n = 86$, which are only indirectly connected with one another. The only logical explanation of this anomaly is that many species of *Drimys* lived in a continent intermediate between South America and Australia namely, Antarctica, during the Cretaceous before that continent became covered with ice. Probably, therefore, the fossil forms that might provide clues of relationship between these widely separated species of *Drimys* are buried under 2,000 meters or more of Antarctic ice. All we can say now is that new knowledge of continental movements based on plate tectonics, as well as molecular knowledge based on nucleic and amino acid sequences of key molecules concerned with floral development, may bring us nearer to a solution of Darwin's puzzle. This return to Darwin's "abominable mystery" has left us with the likelihood that a few clues do exist toward finding such a solution, but that the mystery itself still remains unsolved.

Chapter 26
The Effect of Molecular Knowledge on Classification and Evolution

The understanding of DNA and RNA rather than proteins as components of genes and regulators of their action was virtually achieved in 1965. During the earlier years following the epoch-making discovery of Watson and Crick in 1953, the implication of these discoveries was confined largely to understanding basic processes as revealed in prokaryotes such as *Escherichia coli*. The first significant application to Metazoa was done by Eugene Harris, as well as Richard C. Lewontin and J. L. Hubby,[1] who found that enzymes thought to be equivalent could be separated by gel electrophoresis into components or families, each component having its own distribution in the population of a species. This technique was applied to plants, particularly by R. W. Allard of the University of California at Davis and his associates. It served to reveal differences between races of the same species, such as slender wild oat, *Avena barbata*, that on all morphological characteristics were thought to be homogeneous. Some geneticists, particularly Motoo Kimura, interpreted the early evidence to indicate that Darwin was wrong[2] and many differences between populations and species believed by others to be based on different adaptive complexes of genes and the guiding action of natural selection are in fact equivalent adaptively so that their evolution has been characterized as non-Darwinian and neutral.

The response to this idea among population geneticists was immediate and violent, so that a long dispute has raged over the relative importance of neutral versus adaptive differences. In my opinion, this dispute is unnecessary. My response as a general geneticist is based on the fact that the discovery of the Watson-Crick model of gene duplication and the principle of differential transcription as the fundamental basis of development is so radically different from everything that went before, that our thinking needs to be completely revised with regard to such matters as natural adaptiveness versus molecular neutrality and evolution.

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1. Stebbins is referring here to the pioneering work of Richard C. Lewontin and J. L. Hubby as set forth in a landmark suite of papers introducing the technique of polyacrylamide gel electrophoresis and launching the molecular study of evolutionary genetics. See J. L. Hubby and R. C. Lewontin, "A molecular approach to the study of genic heterozygosity in natural populations, I. The number of alleles at different loci in *Drosophila pseudoobscura*," *Genetics* 54 (1966): 577–594; and R. C. Lewontin and J. L. Hubby, "A molecular approach to the study of genic heterozygosity in natural populations, II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*," *Genetics* 54 (1966): 595–609. — VBS, VCH

2. Cf. M. Kimura's neutral-mutation theory: (1) "Evolutionary rate at the molecular level," *Nature* 217 (1968): 624–626; and (2) "Protein polymorphism as a phrase of molecular evolution," *Nature* 229 (1971): 467–469, co-authored with Tomoko Ohta. Neutral theory is defined as "[t]he proposal that evolution at the molecular level is primarily determined by mutational input and random genetic drift, rather than by natural selection." Wen-Hsiung Li and Dan Graur, *Fundamentals of Molecular Evolution* (Sunderland, Massachusetts: Sinauer Associates, Inc., 1991): 243. See also its theoretical modeling by Masatoshi Nei and Yoshio Tateno, "Interlocus variation of genetic distance and the neutral mutation theory," *Proc. Natl. Acad. Sci. U.S.A.* 72 (1975): 2758–2760. — VCH

Before Watson and Crick, most geneticists believed that genes consisted of proteins and that protein molecules are highly complex, even though the concept of proteins as chains of certain amino acids was not firmly fixed in the minds of biochemists until the 1940s. Furthermore, geneticists had been so much impressed by the discovery of H. J. Muller in 1927 that mutations can be induced by radiation that they believed radiation to be necessary to break the complex protein molecule and specify a new structure that would act as a mutation. Now all scientists agree that mutations are mistakes in copying the DNA and the recent prominence of chemical induction of mutations by certain compounds that affect the atomic structure of nucleotides has rendered highly likely the probability that spontaneous mutations are due not to drastic revisions of other protein or DNA molecules, but merely to mistakes in copying, that is, imperfect action of the Watson-Crick mechanism. Moreover, physicists and chemists have performed experiments showing that such mistakes can occur as frequently as one in every thousand replication events. If the products of these mistakes all survived, neither individuals nor populations could remain constant for even a short period of time on the evolutionary scale. This means that evolutionists must think not only in terms of the frequency at which mutations occur, which probably is always too high to explain the observed constancy of populations and species, but conversely, the frequency at which mistakes in copying are suppressed.

Evidence that this latter trend of thought best explains the situation includes the fact that some of the enzymes responsible for replication of DNA act also to eliminate defective copies. They could be termed "proofreading enzymes." In addition, such drastic changes within a species, such as the conversion of ordinary cabbage into cauliflower, are now explained as the result of mutations in one or two genes that normally interact to produce flowers from embryonic buds. However, comparisons between the effects of gene mutations common for structure and action across flowering plants reveal that the processes share significance and homology, even in plants as different as the small mustard *Arabidopsis* and the cultivated snapdragon *Antirrhinum*. Further examples of model plants include *Nicotiana* and *Petunia*.

Many additions to knowledge have been obtained since 1995,[3] or at least 10 years after I retired from active service and reached the age of 80. I therefore have to apologize for the relative imperfection of my knowledge about them. Nevertheless, I bring them up because understanding the research is essential for all young botanists, particularly if they wish to develop for themselves new concepts or contribute to our understanding of plant evolution. The most active field of discovery relates to the genetic basis of the pathway from gene to physical character, in other words, answers to the questions of why snapdragons differ from mustards. Why are all flowering plants different from conifers? Why are seed-bearing plants different from spore-bearing plants? The most positive results have been based on research in two very different plant species: the garden snapdragon *Antirrhinum majus*, and the small, quick-growing mustard *Arabidopsis thaliana*. In both of these, the genes have been identified that specify the formation of the organs of the flower. For instance, in *Arabidopsis*, genes may specify the timing and formation of sepals and petals, then a different group specifies the origin of petals and stamens, and yet another group specifies carpels and ovules. These separate functions have been recognized because mutants of certain floral genes arose that affect one of

3. G. Ledyard Stebbins died January 19, 2000, at the age of 94. He entered his ninth decade in 1986, and additions to his autobiography date until 2000. — VCH

them but leave the others unaltered. For instance, there is a gene in *Arabidopsis*, known as *AGAMOUS*,[4] of which mutations have given rise to flowers that develop perfectly through the formation of sepals and petals but are unable to form stamens or carpels. Furthermore, sequencing of the nucleic acid and amino acid order of the induced mutations has shown that these genes have their counterparts in snapdragons so that the battery of genes responsible for floral organ differentiation is strongly similar in plants as different as snapdragons and mustards.

In an attempt to answer the question "How do these genes act?" developmental botanists have run into enormous difficulties because of the complexity of gene interaction during development. Two concepts are simple enough to understand and dominate the whole scenario. The first is that at any one stage in development, the DNA of an organism is only partly active. Some sequences of DNA are producing RNA that gives rise to specific proteins, while other genes of the organism are inactive but become active at other stages. This silence and activation is itself governed by the sequential products of particular genes, so that feedbacks can be expected. In addition, interactions between genes that are active at different stages of development can be recognized.

The evolutionary explanation of these conditions is that in the millions or billions of years in which organisms have evolved, some lines have remained simple and represent unicellular flagellate prokaryotes or other organisms, while others have become complex in various ways, for example, higher plants, fungi, and higher animals. The process of becoming more complex is accompanied by increasing nuclear complexity that produces interactions between various developmental genes. This includes both the acquisition of new genes and the modification of existing ones causing them to differ quantitatively in their activity.

As organisms become more complex they acquire more genes, but even faster, they acquire more different interactions between the genes they possess. Many of these interactions are very similar or subtle so that Kimura's concept of neutral gene mutation is partly maintained. However, all major changes in evolution are the appearance either of new functions or of quantitative differences in that same or similar function. Organisms are kept in tune with their environment because natural selection, as Darwin maintained, favors addition or change in function that in turn adapts organisms to new environments. At present, molecular knowledge has helped biologists to understand evolution in three different ways. The first is at a very early stage and is an understanding of the fundaments of differentiation between individuals, particularly in their development. The second is in understanding the evolutionary tree by means of comparing DNA sequences in different organisms. The third is in removing genes from the nuclei

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4. *AGAMOUS* belongs to the *Arabidopsis* MADS-box gene family. As a C-function floral organ identity gene, *AGAMOUS* affects the formation of stamens and carpels, with the mutant allele indeterminately expressing petals rather than stamens in the third floral whorl, and sepals or an *AG* flower primordium for the gynoecium in the fourth whorl of an *Arabidopsis* wildtype flower. Cf. the following literature as available before 2000:

   J. L. Bowman, G. N. Drews, and E. M. Meyerowitz, "Expression of the *Arabidopsis* floral homeotic gene *AGAMOUS* is restricted to specific cell types late in flower development," *Pl. Cell* 3 (1991): 749–758; J. L. Bowman, D. R. Smith, and E. M. Meyerowitz, "Genetic interactions among floral homeotic genes of *Arabidopsis*," *Development* 112 (1991): 1–20; G. N. Drews, J. L. Bowman, and E. M. Meyerowitz, "Negative regulation of the *Arabidopsis* homeotic gene *AGAMOUS* by the *APETALA2* product," *Cell* 65 (1991): 991–1002; M. F. Yanofsky, H. Ma, J. L. Bowman, G. Drews, K. Feldmann, and E. M. Meyerowitz, "The protein encoded by the *Arabidopsis* homeotic gene *AGAMOUS* resembles transcription factors," *Nature* 346 (1990): 35–39; and M. A. Busch, K. Bomblies, and D. Weigel, "Activation of a floral homeotic gene in *Arabidopsis*," *Science* 285 (1990): 585–587. — VCH

of eukaryotic organisms, inserting them into bacterial cells that promote their replication, and then transferring these genes to another organism, in other words, for a valuable factor such as disease resistance. One example of this is the acquisition of disease resistance by the roots of a grapevine, not by breeding and selection, as was previously the case, but by the transfer of a relevant gene from one organism to another.

Chapter 27
My Relationships with Campus Development

When I was at Colgate, one of the closest friends of my first wife, Peggy, and me was Ann Garrison, the wife of a mutual friend in Fine Arts. One evening, we were speculating on our futures, as all four of us were sure that we would not spend the rest of our lives at Colgate. Ann predicted that I would end up either at Harvard or an equally prestigious campus or at Podunk Agricultural College. I agreed, but none of us imagined that both of these two extremes would figure in my career. Nevertheless, that is in part what happened, but nobody anywhere could predict that my campus at the time of my retirement would be as great a mixture of highly theoretical and nationally prestigious disciplines combined with earthy, practical instruction and research such as exists now on the Davis campus of the University of California. The transformation of our campus from the University Farm to its present state took place chiefly during the first half of my active career on the campus from the year I arrived, 1950, to the year I retired, 1973. For anyone interested not only in high-powered research but also in intellectual development and the impact of a flow of graduate students, domestic and foreign, through our system, these 23 years were exciting in every way.

When I arrived on the campus in the spring of 1950, the undergraduate student body, about 2,500 in number, consisted entirely of those enrolled in agriculture and related subjects. The graduate students were numerous and spread throughout the campus but could not obtain the Ph.D. degree except by spending some time in Berkeley and registering on both campuses. Through the faculty group system, which had been invented and organized at Berkeley, all faculty members had to be elected based on their qualifications to disciplines that encompassed the topics of their theses, such as botany, zoology, plant physiology, or genetics. Until I moved to Davis, the chairman of the Genetics group was ex officio the chairman of the Berkeley Genetics Department. When I accepted the move from Berkeley to Davis, both Vice President C. B. Hutchison and the Chairman of Berkeley Genetics, Roy Clausen, agreed I would become chairman of the Davis Genetics Group and, as soon as a graduate division could be established in Davis, I would be responsible to it rather than to Berkeley. This happened in 1957. Naturally, therefore, I had to become familiar with the work of the five or six geneticists already resident at Davis who belonged to various applied disciplines such as Vegetable Crops and Agronomy, as well as with others who joined the various Davis departments after I did. This made it necessary for me to become as well acquainted as I could with graduate students in various disciplines that included genetics. I also became acquainted with many undergraduates because the general course in genetics that Mel Green and I organized was a requirement for undergraduates in the Life Sciences. Many of these students were preparing to enter the newly founded School of Veterinary Science. In this way, I perforce followed closely and participated to some extent in the remarkable growth and transformation of our campus during the 1950s and 1960s.

This growth was much encouraged, not only by Vice President Hutchison but also the two presidents of the statewide system, first Robert Gordon Sproul and then Clark Kerr. The nature of this growth can be illustrated by the new departments that were founded during this period. Among the many changes taking place was the establishment in 1950 of the School of Veterinary Science upon the completion of its home, Haring Hall. At about the same time, departments were founded in Fine Arts, Music,

Philosophy, and other fields. Library facilities were expanded during this period to make advanced education and research in these fields possible by the energy and far-sighted vision of Richard Blanchard, who was librarian from September 1, 1951, until his retirement on September 3, 1974. The chief campus officers who directed these changes were Knowles Ryerson, Stanley Freeborn, Emil Mrak, and James Meyer. Departments of Mathematics, Physics, and Chemistry had been established in the 1920s because they were necessary for agricultural students. Instruction in home economics began at Davis in 1936, becoming the independent Department of Home Economics in 1953. In a later period of transformation in 1965–66, it was disbanded and the programs and faculty were disbursed into three areas: Consumer Sciences (which later became part of the Division of Textiles and Clothing), Nutrition, and Applied Behavioral Sciences.

Other indications of the remarkable change that took place were the replacement of the hog barns by a nuclear reactor belonging to the Department of Physics; the relocation of the amphitheater of cattle judging across the campus and its conversion into a Shakespearean theater in the round; and the replacement of the rather small-shingled recreation hall on the edge of the quadrangle by a large, well-equipped auditorium, Freeborn Hall. Other buildings needed for the expansion were Robbins Hall for Botany, Storer Hall for Zoology, Hutchison Hall for Microbiology and Plant Pathology, Hoagland Hall for Soils and Nutrition, Cruess Hall for Food Chemistry, Asmundson Hall for Avian Science, Voorhies Hall for Economics, Olson and Sproul Halls for Literature and Humanities, the Music-Art-Drama Complex, and Briggs Hall for Entomology, Animal Physiology, Genetics, and Biochemistry.

All of this expansion affected me with respect to my social life as much or more than my professional career. This result came about to a large extent because of a joint interest that developed with my second wife, Barbara, in 1958. Soon after we were married, she founded an off-campus institution, the Davis Art Center, of which the directors were either University faculty members or their wives. I discovered from her difficulties with them that artists, as much or more than scientists, are prone to personal feuds. The center flourished in spite of them, but Barbara's participation declined as the feuds became increasingly difficult for her to tolerate. We became cosponsors of the All-University Concerts series and were equally interested in the plays staged by the Drama Department. Among the plays I particularly remember was a modern-dress performance of Shakespeare's *As You Like It*, in which the exiled duke was transformed into a modern guru and his associated exiles sat in a circle and acted like devotees of the cult of personality. I remember particularly two choral productions because I had already performed the same works while I was at Harvard: Brahms' *German Requiem* and Beethoven's Symphony No. 9.

More recently, the *Requiem* was produced by the University Chorus in 1990, under the direction of Albert J. McNeil, who had an African-American heritage. He did things to it that I liked very much but were frowned upon by most of the musicians of the Music Department. When the Harvard-Radcliffe Chorus performed the work in 1925 under the direction of Sergei Koussevitzky, several music critics complained that Brahms was too boring for the modern age, and a similar verdict had been pronounced by the dramatist and music critic George Bernard Shaw. It is a wonderful piece for a chorus to perform even if its effect on listeners may not be very exciting. In his performance, McNeil changed the rhythmic flavor of the second movement where the chorus sang the text, "The redeemed of the Lord shall return again … in the joy everlasting," to sound almost like a spiritual. In the sixth movement, which begins "We on earth have no continuing place, how beit we seek one to come?" McNeil directed a detachment between each word, creating a feel that the singers were seeking something. Brahms' old lady was therefore the same in form, but decked out with a new spirit of adventure, as are some modern old ladies.

Beethoven's Ninth Symphony was directed by D. Kern Holoman in the 1980s, after both the orchestra and chorus had been vastly improved over their state in the 1950s. The performance, which filled Freeborn Hall by attracting a large number of concert-goers from nearby Sacramento, was brilliant and professional in all respects. I followed it *sub rosa*, silently articulating the tenor parts. In addition, the orchestra had two percussionists, a young man and woman who participated with enthusiasm in the timpani solo in the second movement with a striking effect on the audience.

The intellectual broadening of the Davis campus affected these friends Barbara and I enjoyed during those years. Our closest friends were Jack and Mary Major. He was an ecological botanist with whom I took many trips and collaborated on an important study of endemism in the California flora[1] that has been very often cited and has become a standard reference for botanists in this topic. Mary was not a botanist, but for many years was an active supporter of the Friends of the Davis Arboretum, not only obtaining financial support for this campus institution that serves in place of a botanical garden but also by helping train docents, volunteers who assist the faculty and guide Arboretum visitors. For a number of years, I led these docents on a trip to what is now Stebbins Cold Canyon, a natural reserve that was dedicated to me. We also had in common a number of members of the Music and Fine Arts Departments. A memorable and wonderful spin-off from this connection took place because Davis offered few facilities for entertaining visiting celebrities who performed in the department's Artist-in-Residence Program.

I remember in particular one party in this connection that brought us in contact with an eminent visitor. This would not have been possible on a larger campus like Berkeley. The performer was the internationally renowned pianist Paul Badura-Skoda. His concert was attended by a large audience that filled Freeborn Hall and probably included all piano teachers and students in the surrounding area. At the concert's end, the enthusiasts called forth from him several encores. Finally, with a twinkle in his eye and a glance at a cluster of young people who were gathered near the foot of the stage, he said, "This is my last encore. It is a little-known march by W. A. Mozart." He then plunged into one of the most familiar of Mozart's works, the "Rondo Alla Turca" from Piano Sonata in A Major K. 331, over which doubtless many of his audience had struggled, and gave the most exciting performance of this warhorse that I had ever heard. I was as much fascinated by the rapt expression of his listeners, particularly of the younger ones, as in the performance itself.

Shortly afterward, Barbara and I performed the delightful duty that we had been assigned, to entertain Mr. Badura-Skoda in our home. During the evening, the conversation centered on Schubert sonatas, one of which he had played during the recital, and he told us about his new experiences with them. When the discussion with our musicians had reached a certain point, he said, "I'd like to give you an illustration of this," and sat down at our grand piano. So the evening ended with an internationally renowned musician performing one of his favorite works for us and our friends in our own home. Later on, I realized that this unforgettable experience could not have taken place in Berkeley or on any other major campus, where as a botanist I would have been a smaller fish in a great big pool.

Another series of events that took place during this period were performances of Gilbert and Sullivan operettas, chiefly by amateurs who belonged to the faculty. The principal male part was sung in the rich tenor of a member of the veterinary school, while the parts of middle-aged women that Gilbert enjoyed lampooning so much were

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1. G. L. Stebbins and J. Major, "Endemism and speciation in the California flora," *Ecol. Monog.* 35 (1965): 1–35. — VCH

sung by Amy Patten, the wife of a physics professor. Among all of the Gilbert and Sullivan performances, those of Amy as Little Buttercup in *H.M.S. Pinafore*, Ruth in *Pirates of Penzance*, the Fairy Queen in *Iolanthe*, and Lady Jane in *Patience* are among my most treasured remembrances.

Chapter 28
Doby at Davis

In 1969, both the then-Chairman of Genetics, Bob Allard, and I received word that my close friend Theodosius Dobzhansky was about to retire from his position at the Rockefeller University in New York. Although he was given an option to remain as a retiree, he would no longer be supplied with a laboratory, and his close assistant, Francisco Ayala, would have to go elsewhere. Furthermore, Dobzhansky had just lost his wife and so if he stayed in New York, he would be relatively lonely, as he had not become close to scientists at Rockefeller. Allard made informal advances to Doby and learned that if we could have both him and Ayala appointed, they would both come to us. At this time, Briggs Hall was almost complete and we were able to provide room for two new faculty members. Consequently, Allard and I approached our administration asking if Doby could become attached to our faculty and if space could be given him to continue research on a grant that he already had. This space was next to one that would be occupied by Ayala, assuming that he would also be appointed. This bold and complex plan eventually worked out. However, before Doby could come to us on a permanent basis, all of these arrangements had to be made. We therefore took advantage of the fact that our department had been awarded a training grant from the National Institutes of Health that would provide a salary but not living expenses for a visiting professor. I realized that this would be a fine opportunity for me to repay the hospitality that Doby and Natasha had given me in 1946 at their New York apartment. I asked Barbara if Doby could stay during this period in a spare room in our large house, and she assented. I had qualms about doing this because both Barbara and Doby were rather particular and I didn't know how well they would get along together. However, I needn't have worried. Ayala was first appointed to the tenure position of Associate Professor, while Doby was promised space in Briggs Hall and subsisted on his pension from the Rockefeller University as he did not receive a salary at UC–Davis.

During the spring of 1970, Doby won the favor of our graduate students and his lectures were a great success. He was very much indebted to Barbara for her hospitality, and they had in common an interest in classical art and opera. Barbara was delighted to help him locate a lot in North Davis where he could build a duplex house in which he would occupy one half, and the other half would be occupied by his technician and research assistant, Olga Pavlovsky, with her husband, Vadim. Finally in June, the time came for Doby to wind up his affairs in New York before coming to us in the autumn.

One afternoon while we were walking to the campus, Doby said, "I want to do something very nice for Barbara because she has done so much for me."

I thought for a moment, then ventured, "She would be delighted with a well-illustrated gift volume of classical art."

"That wouldn't be good enough," Doby responded. "I would like to get her something that she can use and enjoy every day."

I thought a little further and then said, "We have a cabin at Wright's Lake in the Sierra. Barbara would very much like to have a canoe that we could paddle on the lake."

"Excellent!" he said. "You order the canoe. I give it to her." I borrowed a catalog from a friend and picked out one that would be appropriate. Unfortunately, Doby had to leave for New York before it arrived but nevertheless showed Barbara a picture of it, and it was at our cabin by the time he got back in September. We were debating as to

what we were to name it, and Barbara strongly recommended that we named it "Doby." I asked him if he would accept that proposal even if it resulted in our telling ourselves many times while there, "Let's go out and paddle Doby." He said yes, of course.

After I knew that Doby, Francisco Ayala, and I would be together for a number of years, I realized that this situation would present an opportunity to write a multidisciplinary book on evolution that would result from a collaboration between four authors, and therefore could be fully modern in every respect. Doby would present classical evolution and human evolution, Ayala would present some modern molecular aspects, particularly allozyme markers, I would present plant evolution, and then we would need only a fourth author to present paleontological evidence. Doby, Francisco, and I agreed that this would be a good idea, and we found our fourth collaborator in James Valentine, who was at that time in our Geology Department.

The editors of W. H. Freeman and Company accepted our proposal with alacrity and we made plans to put it together. This collaboration began in 1971, when Doby and Ayala organized a small symposium of experts in the philosophy of evolution, held at the Rockefeller-owned Villa Serbelloni on Lake Como in Italy. There we found that the environment was particularly favorable for collaboration without outside disturbance and so applied for a residency for each of the four of us at the villa during the summer of the following year, 1972. Unfortunately, Doby felt that he could not stay there for the long time necessary for collaboration, so the three of us worked together during that period and went back to Davis to complete the job. This took several years, during which Francisco became so busy with his university position that we had to wait for his manuscript, and then Doby became increasingly unwell.

Finally, in December 1975, Barbara and I invited Doby to our home for a party that included just us, the departmental secretary, and Doby's assistant, the successor to Olga Pavlovsky. During this party, Doby seemed to be weaker than usual and when we said goodnight he commented, "I'm afraid that it won't be long now." The following morning he was taken violently ill in his apartment and the student who was occupying the neighboring apartment telephoned Ayala, who arrived as quickly as he could. While Francisco was driving Doby to the hospital, Doby died. He didn't live to see the publication in 1977 of our four-author book, *Evolution*. It had a moderate success but was soon superseded by other textbooks that were more strongly oriented toward molecular biology.[1]

The year 1973 was the last of my active service before formal retirement. It was also the first year in which the administration decided to encourage teaching on the campus by presenting an award to the Teacher of the Year, selected from faculty members in all or nearly all of the academic disciplines: literature, history, political science, sociology, philosophy, art, music, and natural science. These awards have been given every year until the present. Among the five faculty members selected for the first award, I represented the natural sciences.

Late in 1979, our Chancellor, Jim Meyer, telephoned to ask me if I would agree to have a newly acquired reserve named after me. I was much pleased to accept and then discovered it was in Cold Canyon, a tributary of Putah Creek in the Inner Coast Range just below the Lake Berryessa dam in California. It had been acquired from the estate of a private owner who had used it for grazing sheep several years before. The tributary had recovered from this damage, and it now offered a good opportunity for botanists, zoologists, and entomologists to make afternoon trips with their classes and to carry out

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1. Th. Dobzhansky, F. J. Ayala, G. L. Stebbins, and J. W. Valentine, *Evolution* (San Francisco: W. H. Freeman and Co., 1977). — VBS

various kinds of research projects. With my colleague Jack Major, I went shortly after acceptance to visit the area and was impressed with its possibilities. Although it did not contain any rare or endangered species, its flora was relatively undisturbed and offered many kinds of opportunities for research on pollination, seed dispersal, and the comparative ecology of species of native annuals. In 1981, we had a formal dedication, followed by many visits from various field biologists. It appears to be a bird watcher's paradise. At the dedication, I was reminded of words I'd heard from a colleague from Berkeley, Curt Stern, shortly before he became disabled and passed away. He had been asked to take part in the dedication of a building on the Berkeley campus to the eminent molecular biologist, Wendell Stanley. Stern had remarked wistfully, "At my age, all my friends are turning into buildings."

I repeated this quote and added, "At my age, I am happy to know that I will not turn into a dead building fashioned from stone, but will turn into a carefully guarded preserve, vibrant with life, where future students can do research and make efforts to answer questions and solve problems that I have been unable to do."

Since then, the area has been subjected to a few disasters, including two landslides that swept away some of the original vegetation and a fire that fortunately did only superficial damage. The canyon is still much visited and enjoyed by nature-loving people, and several important research projects have been carried out there. I decided this would be the resting place for my final ashes where they would join those of my dear wife Barbara.

About the same time, a most welcome message came from a different direction telling me that I had been awarded the National Medal of Science, the highest award that a United States scientist can receive from his fellow countrymen. In the spring of 1980, I went to Washington, shook hands with President Jimmy Carter, and accepted the medal from him. This medal had already been awarded to my fellow evolutionists Theodosius Dobzhansky and Ernst Mayr, so I particularly enjoyed joining their illustrious company.

Chapter 29
Around the World in Five Springtimes

In 1973, our campus declared that the normal retirement age would be reduced from 70 to 67, thereby making me eligible for retirement in July of that year. Although they did give me a chance to continue on a year-by-year basis, I discovered that I had opportunities to spend my early retirement years as a visiting professor at various institutions throughout the world and so decided to take advantage of these opportunities.

The first of them was made possible by an arrangement between the University of California and the University of Chile, known as the Convenio, to invite professors from California to spend a year in Santiago and for Chilean students to come to various UC campuses. As another opportunity, I was able to make arrangements with the French geneticist Georges Valdeyron to spend the spring of 1974 at the Institute Écologique Emberger in Montpellier, France, and with the Australian Government to be a research and teaching visitor at the Australian National University in Canberra.

Considering that I would spend the spring of 1973 and again in 1975 at home in Davis, I decided that this flourish of visits could be called, "Around the World in Five Springtimes": California, Chile, France, Australia, and again California.

Consequently, in July 1973, I flew to Santiago and was greeted by Eduardo Zeiger, who, after receiving his Ph.D. under me, had become established at the University of Chile. He first took me to an apartment building that was permanently rented by the Convenio in the more fashionable suburb of Santiago. The on-site manager of the Convenio, Roy Fry, and his wife occupied one of the apartments and made others available to visitors. Barbara had held for many years an aversion to flying, so she went by freighter and did not arrive until I had been in Santiago for more than a month. For most of this early interval, I had a roommate who was attached to the Davis Agronomy Department. Eduardo Zeiger took me to the University, got me established in an office, and explained what he expected of me, as he was not only a professor of biology but also chairman of the department. I was to give a course in evolution and to engage in joint research projects with students as they became available.

Eduardo told me that Chile was in a precarious political state because its duly elected president, Salvador Allende, was very liberal and sympathetic to communists if not actually a communist himself. This made him very unpopular with businessmen, both Chilean and North American, who were interested mostly in maintaining a flow of copper to our country from the rich deposits in northern Chile. Furthermore, apparent inefficiency in transportation had reduced to a minimum the supply of foodstuffs of various kinds in the markets and had caused gasoline to be strongly limited.

One important feature of my course was to be field trips, to prepare for which I would have to locate suitable projects as quickly as I could. An obvious one hit me as soon as I was first being driven into areas around Santiago, as throughout central Chile the plant that dominated the margins of highways is the introduced California poppy *Eschscholzia californica*.[1] If we could find variability in its populations that might be

1. The Jepson Manual notes this poppy as highly variable in California, listing in addition to *Eschscholzia californica* Cham., *Eschscholzia californica* subsp. *mexicana* (Greene) C. Clark and *Eschscholzia procera* Greene. J. C. Hickson, ed., *The Jepson Manual, Higher Plants of California* (Berkeley: University of California Press, 1993): 814. — VCH

related to variability in the populations of California, this would be a great bonus for both Chilean and North American botanists. A glance at a few populations showed at once that variation from one plant to another in characteristics of the flower was ample and that differences exist between populations.

Furthermore, the genetics of flower color had been worked out by North American botanists, and Stanley Cook, a student of my colleague Herbert Baker at Berkeley, had carried out a careful comparison of different populations of central California. With a Chilean assistant, I therefore explored populations in central Chile and seemed to find agreement with the situation described by Cook. Flower color in both varies from deep orange to pale orange or even yellow, and the paler individuals often had petals that had a deep yellow or pale orange spot at the base, a pale middle area, and orange tips. I decided that we would have a series of field trips to explore this problem. These were so successful that at the end of the course, I collaborated with six of my students to write up the situation. We had found that populations from the more mesic area east of Santiago at the foot of the Andes, as well as some of those to the west near the coast at Viña del Mar, had flowers that were predominantly deep orange. However, the dry areas to the northeast of the Santiago Valley near the Acongagua River were dominated by pale flowers, including many with an orange center and paler margins. This discovery seemed to be a contrast to the pattern found by Cook in central California[2] where the interior coastal valleys and neighboring hills have orange populations, while the dunes along the moist, foggy coast have populations that consist chiefly of plants bearing flowers with orange centers and yellow margins. In other words, the ecological trend in Chile was clearly from orange flowers in the more favorable parts of the range and paler colors in regions exposed to greater drought stress. We proposed several hypotheses to explain this apparent difference involving chiefly a shift in relationship due to drift in the small initial populations in Chile so that deep color, which in California had been associated with the warm dry interiors and paler color plus central spots on the petals with the cool coast, had become associated in Chile with dry rather than moist conditions.

When I got back to California and started to check up on our speculations, I discovered that we had interpreted the facts wrongly because Cook's study had dealt only with populations in the Coast Ranges, while a glance at populations of California poppy in the Sierra foothills revealed quite a different situation. In the latter area, California poppies are rarer than they are on the coast but do occur in areas underlain by serpentine formations. These populations on serpentine that occur in more stressful areas than do any of the populations studied by Cook, resemble the stout, tolerant populations in northeast Chile in possessing predominantly pale-colored flowers often having an orange central area.

This situation obviously needs more study in California concentrating on the Central Valley and the Sierra foothills, the area from which seeds most probably were taken by Chilean miners returning to their homes from the gold rush area. As the California poppy is also a popular garden plant in Chile, seeds of large, orange-flowered individuals may have been sent from California seed nurseries. A re-examination of California populations emphasizing those of the Central Valley and Sierra foothills and subjecting plants to biochemical analysis for allozyme difference would be highly appropriate. This situation appears to me to be a typical example of misapplication of Occam's razor, which states that the best explanation of any natural situation is the simplest one. This aphorism is excellent if one is sure that one has all of the necessary facts. A more general and superseding aphorism is that if the available facts are not all those that exist, Occam's razor is more likely to cut one's own scientific throat than to provide the solution of a problem.

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2. S. A. Cook, "Genetic system, variation, and adaptation in *Eschscholzia californica*," *Evolution* 16 (1962): 278–299. — VCH

A problem involving speciation and hybridization was presented by the genus *Colliguaja* belonging to the family Euphorbiaceae, a common shrub in central Chile. It contains two species in this area, one of them with relatively broad leaves found mostly in the coast ranges and the other with narrow leaves found chiefly in the interior. They differ also with respect to characteristics of the inflorescence and flowers, which I shall not enumerate. Wherever populations of the two different species are near each other, occasional backcrossing and introgressive individuals are found. The whole situation is ideal for illustrating the methods and ideas of Edgar Anderson with respect to hybridization and backcrossing in habitats where hybrid and backcross individuals are better adapted to certain sites than are individuals belonging to either one of the parental species.

The political instability of Chile during this period became obvious to me as I looked at the almost-bare shelves in the grocery stores and waited in line at gas stations to get enough fuel even for a modest amount of driving in the vehicle that the authorities had provided me for my stay. My roommate in the rented apartment, on the other hand, could bring back to us very fine vegetables and meats that he got from the farmers immediately surrounding the rural experiment station where he was doing his research. Obviously, the weakest link in Chilean society under Allende was commercial transportation. I had learned that even though the filling stations in Santiago were always shy of gasoline, large storage tanks on the coast near the commercial port of Valparaíso were full of fuel.

The situation came to a head about a month after my arrival, the 11th of September, a day that was perpetuated for the next few years as "El Once."

While I was delivering, in the best Spanish that I could muster, a lecture on the biochemistry and functioning of DNA, I noticed a considerable level of uneasiness among the students. Then one of them came in from outside and shouted, "Golpe del estado" (coup d'état). Immediately the class broke up, and one of the Chilean faculty recommended strongly that we go home and wait there for what was going to happen. On the way home, I passed a high school and offered to its students a ride to my area. Immediately my car was filled to overflowing by anxious students wanting to get home. When I got back to our apartment building, Mrs. Fry told me that her husband was in Los Angeles at a business meeting. Another North American, zoologist Rob Colwell, who occupied the apartment next to mine, was waiting for his wife,[3] who planned to arrive that day from San Francisco. We eagerly listened to the radio for developments. At first, the radio was controlled by Allende supporters, who called upon loyal supporters to go to their assigned posts at this time, then the radio went dead for one or two hours. We learned from other sources that supporters of a military junta, led by General Augusto Pinochet plus a naval admiral and an air force commander, had forcibly entered the parliament building in the middle of Santiago and that Allende either had been killed or had committed suicide.

Which of these two fates Allende suffered was never clear. We telephoned friends in the center of the city about five miles away and discovered that a general revolution was taking place there with at least some casualties. The little group in our apartment complex was joined by the wife of a surgeon who had survived the coup and was taking care of the casualties. When the radio went on again, we heard martial music followed by a new voice that proclaimed a curfew and warned everybody to stay in their homes

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3. Colwell's then-wife, Mary-Claire King, had just received her Ph.D. in genetics from UC–Berkeley. She later pioneered research in hereditary breast cancer and in 2006 received the Dr. A. H. Heineken Prize for Medicine, the Weizmann Women and Science Award, and the Peter Gruber Foundation Genetics Award. Dr. King worked to identify children kidnapped during Argentina's military dictatorship in the 1970s and to reunite them with their families. — EPD

until further notice. We were therefore imprisoned in our apartment complex and could not reach our spouses, consisting of Roy Fry in Los Angeles, Mrs. Colwell in Buenos Aires waiting for the resumption of flights to Santiago, and Barbara on a ship being prevented from entering Chile by border guards.

Actually, our imprisonment was a pleasant one. Mrs. Fry's apartment contained enough food to last several days, and the wife of the surgeon was an expert gourmet cook. Mrs. Fry was afraid to telephone a friend who had a ham radio, but we went to his home a few blocks away, and she asked him to make contact with her husband in Los Angeles if he could. He was rather dubious but said he would try. We went back to our apartments and waited for eventualities. Much later, the ham radio operator said he had sent a notice without stating the radio number and said simply, "Fry in Los Angeles, come in if you can. Your wife and friends are free and well." We, therefore, had as pleasant a stay in the apartments as we could for the three days before the daylight curfew was lifted. Meanwhile, the Colwells were reunited, but I was still waiting for Barbara's ship to sail around the southern tip of South America and up to Valparaíso, where I was to join her.

The first result of the coup was the suspension of all activity in the university because of the large number of Allende sympathizers that it contained and that the Pinochet administration was committed to weeding out. Nevertheless, I had a friend who enabled me to continue my course during this critical period. He was Danko Brncic, a Chilean of Slovak origin who had received his Ph.D. degree under Doby at Columbia and was professor in the medical school at the other end of Santiago from the university proper. Like most medical schools, it was conservative with respect to its faculty, including Danko. We therefore met in his department for about a month until the situation at the university became better.

The most critical event of the whole affair came during this period. One morning my Chilean colleague and I were just ready to go on a scouting trip for another population of California poppy, when a fleet of military jeeps descended on the university and commanded us to go into the central courtyard, where they flattened us against the side wall with our hands held up and our backs to the military officials issuing commands. While we were thus pinned up and unable to speak, they read out the names of suspects whom they would either banish from Chile or put into a concentration camp that had been hastily put together on the soccer playing field. I recognized the names of several friends from UCLA whom I knew had come down to associate with the Allende group and correctly assumed that they would go back to our country in the very near future. Finally, we were commanded to turn around and present identification. As a sergeant was beginning to look at our papers, I realized that I did not have a Chilean identification card, even though two weeks earlier I had submitted my passport to the foreign office of the Allende government and had asked them to prepare for me a Chilean identification card. They were so dilatory in performing this service that, although they had given me back my passport, they had not prepared the ID before they were overthrown by the coup. When the sergeant came to me, I explained this situation and handed him my U.S. passport. He looked very severe and without hesitation or a word to me, took the passport over to a group of officials who were deciding what to do with us. This was the most apprehensive moment I have ever had in my life. I began to see myself either summarily shipped back to the United States or joining the others in the concentration camp. However, there were faculty members of the university to whom the military turned for advice. One of them was asked for his opinion. Although his last name was Izquierdo, which means left, he actually was on the right side so far as the military was concerned. I gasped a sigh of relief when, after being shown my passport, he nodded approvingly and my document was handed back to me by the sergeant without comment. After that, I lived a reasonably normal life there until the end of my stay, except for a 7:00 p.m. curfew.

Shortly after that incident, I received word that Barbara's ship was about to arrive in Valparaíso and so went down to meet her. The reunion was loving on both sides. Then after our joyous greeting, we had the job of getting Barbara and her baggage through the special detention and customs office that had been placed on the highway at the entrance to the valley of Santiago. Barbara had a good deal of baggage that was carefully screened by a couple of severe-faced officers, but they did not find anything to which they objected. When they had finally given us papers to sign and signed their approval of us and our cargo, Barbara pulled out a package from under the seat of our vehicle and opened it. There, spread out before the officers, were Havana cigars that she had bought in Rio de Janeiro for just this purpose. Their eyes lit up and their frowns changed into grins as they eagerly accepted these rarities, which she had been careful to hide from them until all of our signatures were firmly established on the papers, so that nobody could accuse us of bribing them. This bit of diplomacy was characteristic of my dear wife.

Toward the end of our stay, we contacted the parents of several students who had approached us before we left the United States and had asked us to bring gifts to deliver to their parents. When we asked their parents how could we deliver these gifts, they responded by inviting us to a splendid evening party for which we could get permission to stay with them after the curfew. During this party, one of them asked me how I liked their country. While expressing gratitude at our personal reception and at the natural history and flora of their country, I said I hoped that they would soon have democracy again. They were apparently so conservative that they liked the Pinochet regime and criticized us for not approving of it. At that, I couldn't help a breach of diplomacy and tell them that if their present situation kept up, their country would degenerate into another Nicaragua or Paraguay. Apparently, there must have been many Chileans who felt as I did, because eventually Pinochet was deposed and the country now is reasonably democratic.

In addition to my teaching and research, I also took advantage of my stay in Chile to acquire personally more information about its flora, in particular its relationship to that of California. Another impetus for understanding better the flora of Chile was my remembrance that I would be following in the footsteps of my scientific patron saint, Charles Darwin. Before leaving Berkeley, I had read with particular interest Darwin's description of his scientific explorations in Chile. Among them was the climb of a mountain east of Valparaíso known as the Sierra de Campaña, on the summit of which the Chileans have placed a small monument in Darwin's honor. A pilgrimage to this spot was of historical interest, but as the only chance I had to go there was too early for the development of the flora, I could not make a direct comparison with Darwin's investigation. A second area that he emphasized was the pass through which he crossed the Andes from Chile to Argentina. I took a day trip to this pass from Santiago late enough in my stay so that I could see something of its flora, particularly the species of *Senecio* or groundsel that are also mentioned prominently by the British plant geographer, J. C. Willis and his colleague Dr. James Small.[4] On the basis of Willis' age and area theory, Small recorded the fact that *Senecio* is the largest genus of the family Asteraceae and that the Andes possessed the greatest diversity of species found anywhere in the world. He therefore concluded that the family Asteraceae originated in the Andes during the Cretaceous period. Unfortunately for his theory, the Andes had not been uplifted during the Cretaceous,

4. James Small, a lecturer in botany at Belford College, London, and later a botany professor at Queen's University of Belfast, put forth the treatise *The Origin and Development of the Compositae [Asteraceae]*...published in 1919 (London: William Wesley and Son, *New Phytol. Reprint,* No. 11, 334 pages). John Pruski, pers. obs. — VCH

while other evidence indicated that the Asteraceae did not originate until after the end of the Cretaceous. I spent a small amount of my time looking for another explanation of the diversity of *Senecio* in the Andes and in particular at the latitude of Santiago. I first read descriptions in the literature of species that occurred there and got a glimpse of them during my day in the region where they are abundant. These observations show that the Andean species of *Senecio*, though numerous, are all very much like each other, and represent only a small sample of the diversity found in the genus. When I saw them in their native habitat, they reminded me very much of species of hawkweeds in *Hieracium* and pussytoes in *Antennaria* that were known to be apomictic clones of hybrid origin. I suspect that this is true also of the Andean species of *Senecio* and believe that a careful cytogenetic study of the species supplemented by allozymes and DNA markers would clear up the problem.

In addition, I looked particularly at such aster genera as *Clarkia*, *Microseris*, and *Blennosperma*, in which one or two Chilean species are closely related to others in California. I was particularly interested to see whether the other plants associated with these Chilean species also had closer affinities with Californian species than with their companions in Chile. What struck me on the whole was that these species behaved as if they had been introduced by humans, even though there was very good evidence to indicate that they had been in South America before Europeans arrived. Apparently, their presence in association with European introductions suggested that the native flora had been put together from various sources. If we knew more about its history, we would find that the present assemblage has been put together at various times and under diverse conditions.

Such examples of long-distance dispersal may be the result of accidents involving animal visitors. For instance, among the numerous migratory birds, some might be so weakened by the long distance of travel across the equator that they would be easy prey for various predators. If they had been killed by predation, seeds that had avoided digestion by remaining in the bird's crop during the long flight could fall to the ground and produce seedlings, particularly in areas of habitat disturbance. In my speculation about these situations, I had already suggested the presence of three specific vectors that I designated as the "slovenly plover," the "sloppy phalarope," and the "constipated Arctic tern." The first of these would be the bird the golden plover[5] that regularly migrates from Alaska to Hawaii. This might explain the presence of a subarctic species of English sundew *Drosera anglica* in a bog on the summit of the island Kauai in Hawaii. The sloppy phalarope[6] would have belonged to a species of bird that migrates from the Great Basin region of the United States to southern Chile and Argentina. Their exact distribution, both in the mountains surrounding the Great Basin and the cold steppes of Patagonia, corresponds to a series of all-female apomicts belonging to the pussytoes in *Antennaria* and having sexual relatives in the Rocky Mountains of Montana and Wyoming. The constipated Arctic tern may be a complete fiction,[7] as terns normally feed on fish rather than vegetable matter. It might, however, have been a tern that had bad luck fishing and had eaten berries to save itself from starvation. The example of long-distance dispersal, however, is very definite because it involves the black crowberry

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5. Two golden plovers are noted to migrate across the Americas. *Pluvialis dominica* Muller or the American golden plover is more frequently seen than *Pluvialis fulva* J. F. Gmel., the Pacific golden plover. D. A. Sibley, *The Sibley Guide to Birds* (New York: Alfred A. Knopf, 2000). — VCH

6. Three phalaropes migrate in the New World: *Phalaropus tricolor* Vieillot (Wilson's phalarope), *Phalaropus fulicaria* L. (red phalarope), and *Phalaropus lobatus* L. (red-necked phalarope). Wilson's phalarope is a summer resident of the American Great Basin. D. A. Sibley, *The Sibley Guide to Birds* (New York: Alfred A. Knopf, 2000). — VCH

7. Nonetheless, the Arctic tern is quite real, known as *Sterna paradisaea*. D. A. Sibley, *The Sibley Guide to Birds* (New York: Alfred A. Knopf, 2000). — VCH

Empetrum nigrum that is very common all around the Arctic but south of the equator occurs only at the southernmost tip of Argentina and Chile.

Another feature of the Chilean flora that I observed both in lowlands and at higher altitudes was the presence of woody plants belonging to families that are usually regarded as chiefly tropical. One of these is the Icacinaceae to which belongs the species *Villarezia mucronata* that occurs near Valparaíso at the same south latitude as is the north latitude of Los Angeles. Others belong to the Monimiaceae and Lauraceae. A still different situation at the latitude of Santiago is the unusual phyletic position of the woody plants found on the ridge of the Andes immediately east of Santiago at the highest altitudes at which woody plants are found. These include a species of *Fabiana* (in Solanaceae), another of *Eccremocarpus* (Bignoniaceae), as well as those of *Colliguaja*.

The occurrence of these species suggests that the northern limits of these genera in North America may be determined chiefly by the amount of frost and snow to which they are exposed during the winter. It is an interesting fact that although Philadelphia and Valdivia are located 40 degrees north and south, respectively, away from the equator, the forest in eastern Pennsylvania is composed of deciduous trees while that of Valdivia consists entirely of broad-leaved evergreens plus one conifer genus, *Fitzroya*. The differences are probably related to the large amount of ocean versus land in the Southern Hemisphere and the preponderance of land over ocean in the Northern Hemisphere.

My teaching assignment in Santiago ended with the beginning of Christmas vacation at the university, but before leaving I took three very interesting trips. The first of these was with members of the forestry section of the university to an area in the south-central Andes near Concepción. These mountains were sufficiently far south to be in the area of four-season moisture and to support a forest consisting principally of species of the southern beech *Nothofagus*, the forest with both broad-leaved evergreens and deciduous taxa.

A very interesting feature of this forest is the occurrence of epiphytic species, those growing on trees, belonging to the family Myzodendraceae that look very much like the Spanish moss *Tillandsia usneoides* that hangs from trees in the southeastern United States, as well as species of lichens belonging to *Alectoria* and *Usnea* that are also called Spanish moss in central California and beard moss in northern coniferous forests.

The use of this common name for these very different species of plants in the southeastern United States and California is glaringly inappropriate in both places as neither of them is Spanish nor a moss. The borders of the Chilean forest are occupied by species belonging to subtropical genera of Myrtaceae and a primitive species of angiosperms, *Drimys winteri* in Winteraceae. Open glades in this forest are occupied by shrubs or small trees belonging to the family Proteaceae that otherwise is characteristic of Australia and South Africa. All of these southern forests probably radiated outward from Antarctica before that continent became covered by glacial ice. I spent three satisfying nights sleeping under a splendid tree of *Drimys*. Winteraceae is regarded by many botanists, including both Armen Takhtajan and Arthur Cronquist, as the most primitive of all flowering plant families.

The last two Chilean trips were both taken in the company of Carlos Muñoz, a well-known expert on Chilean grasses who died shortly after my visit, but who in 1973 was still active although retired and most generous in inviting me to go with him. In early December, we spent a day in the area known as the Norte Chico, 100 to 150 kilometers north of Santiago and in a dry savanna between the Mediterranean climatic area around Santiago and the desert of northern Chile. It is an area that contains many species of restricted distribution corresponding to the area in the Northern Hemisphere between San Diego and northwestern Baja California. The species that I saw all belong to typical

South American genera such as *Calceolaria* (in the Scrophulariaceae), as well as the southern limit of the genus *Larrea* or creosote bush in Zygophyllaceae that is a familiar dominant of our Mojave and Colorado deserts.

The third trip was along the Trans-Andean Highway to the crest of the Andes where it and the Trans-Andean Railroad passed through tunnels to the Argentinean side. Two things impressed me most about this trip. In the first place, the alpine zone at 3,000 meters is much more arid than any comparable zone known to me in North America. There are many cushion plants that belong to genera familiar to Californians such as *Astragalus* and *Calandrinia*, as well as a luxuriant species of *Calceolaria* that grows near streams, and distinctive sharp-leaved cushion plants belonging to the Apiaceae or parsley family are also widespread. The second distinctive feature is that species of certain genera such as *Baccharis* appear to be identical with their congeners that occur at or near sea level.

During the last part of my stay in South America, I was alone again because Barbara wanted to return via Peru and go first to California while I had reservations to fly directly from Santiago to Cannes, France. I met her in Cannes, and we went together by bus, first to Marseilles for the elegant seafood to which we had been introduced by a student of Professor Guinochet, then to Arles to see some of the entrancing scenes made famous by the paintings of Vincent Van Gogh.

We finally arrived at Montpellier and met our host, Georges Valdeyron, at the Institute Écologique Emberger (later the Centre d'Études Phytosocialogiques et Écologiques Louis Emberger). He helped us to find a house in a suburb about four miles away belonging to a staff member of the Institute who was on leave in the United States and from whom we rented the house for our period of stay from January to July of 1974.

Barbara and I much enjoyed our life in southern France, chiefly during weekends when I was not at the Institute. We visited a historic Roman aqueduct that had brought water to the nearby city of Nîmes as well as the city of Avignon, where we went through the palace occupied by the Popes who resided in Avignon during the Great Schism in the Middle Ages, as well as a bridge (le pont) that might have been the origin of the French nursery rhyme and song "Sur le pont d'Avignon." On warm days we enjoyed the nearby beach and during the latter part of our stay had a fine three-day tour through the spectacular Gorge du Tarn, then on to Toulouse and then back to Montpellier.

My scientific project, which Dr. Valdeyron approved and for which he provided space and technical assistance, was a comparison of the species of the bur clover *Medicago* that are particularly numerous in southern France and that I hoped would provide data that would demonstrate correlations between seed productivity and the morphology of the fruits. Unfortunately, I did not realize at that time that many of the species need to be cross-pollinated by insects, and so did not provide the necessary insect vectors. Nevertheless, the visit was valuable to me because of contacts with Dr. Valdeyron and other staff members, and the lectures that I gave at the Université de Languedoc went over very well.

At the end of our stay in Montpellier, we went to Italy and the Rockefeller-owned Villa de Serbelloni, where we met my colleagues Francisco Ayala and Jim Valentine. While Barbara spent her time traveling in northern Italy, Francisco, Jim, and I spent about six weeks preparing and discussing our manuscripts for *Evolution*, the textbook that we were to have published by W. H. Freeman and Company. After our stay was over, we went our separate ways, Francisco, Jim, and Barbara back to Davis and I to a short interlude at a small resort in the southern Alps with my good friend Claude Favarger from Neuchâtel, Switzerland.

From there I headed for England and flew to Perth, Australia, for my next visit of research and teaching. I arrived when a warm winter brought out flowers already in

mid-September, and I passed a most rewarding week in company with the staff of the local botanical garden that is attached to the University of Western Australia. Even though I realized that western Australia has, next to South Africa, the richest temperate flora in the world, I was not prepared for the 400-mile trip north from Perth where I saw the flowering shrubs and some herbaceous plants in their glory. I was able to begin my project for the stay in Australia, which was a cytological investigation of populations belonging to the genus *Hibbertia*. This genus belongs to a family more primitive than any otherwise large shrubby family in the Northern Hemisphere and is also larger than the tropical genera of its family, the Dilleniaceae. All genera of this family have the primitive character of carpels that are separate, with several-seeded follicles.

From Perth, I went to Adelaide, where I was warmly greeted by Peter Martin, who had spent a year with me in Davis. Adelaide is near the southern coast of Australia and at the mouth of the largest river on the continent. With the Martins, we took a day's trip to see this river, the Darling. Relative to the continent, it should be compared to the Mississippi in North America, but the difference between the two rivers is dramatic. Where I saw it, only a few hundred miles from its mouth, it seemed to be no bigger than the Sacramento River in California. This comparison shows as clearly as anything else how much drier is the continent of Australia than any other comparable land mass. From Adelaide, I continued to Canberra and to my lodging on the campus of the Australian National University. This beautiful campus is relatively rural as Canberra was established as a cluster of relatively small cities near enough to each other to permit free exchange between them but far enough apart so that no complex metropolitan area could become built up. What at first struck me as remarkable were the many parrots flitting from one to another of the *Eucalyptus* trees on campus, squawking in their own parrot language.

I found my office in the Biology building through the help of Professor Barney John, whom I had met in England before he immigrated to Australia. I found in the herbarium that Professor R. D. Hoogland had already worked on the systematics of *Hibbertia*, so that during my stay we collaborated in our study of this genus. Although we did not progress far enough to produce a monograph of the genus, we found out enough about it to realize what an unusual position it occupies among flowering plants. Although it is not regarded as equal in primitiveness to such families as Magnoliaceae and Winteraceae, nevertheless its family, the Dilleniaceae, is one of half a dozen families having the primitive condition of separate carpels associated with a primitive woody morphology of its stems and branches. It also contains diploid species having the gametic number of four, six, or eight, a condition that is equaled only by the Annonaceae. Its approximately 130 species are spread throughout Australia and are confined to this island-continent except for a few that are found in adjacent New Guinea. Its diversity with respect to both vegetative and reproductive structures can give us some idea of how different species are differentiated from each other among angiosperms in general. In addition to this research, which was the last in which I made significant discoveries rather than repetitions of discovery that I had made in other genera, I gave a full series of lectures on evolution at the Australian National University in Canberra and visited all of the other important educational institutions throughout Australia for lectures and discussions with faculty members. Like all other botanists, I was astounded at the unusual diversity of the Australian flora for which partial explanations exist but more ideas are needed.

Fortunately, Barbara had overcome her phobia against flying before her trip from Davis to Sydney, and she joined me in November. We explored together some of the principal areas on the eastern side of the continent. The first of these was near Townsville in northern Queensland. We had hoped to visit the famous Great Barrier Reef to

see its phenomenal marine life. We were told, however, that a recent hurricane had damaged the facilities for visitors to such an extent that none were allowed to go to the reef during our stay. We were, however, warmly greeted by Bill Hamner from UCLA and saw the marine station that he was helping to establish. We had hoped also to enjoy swimming off the beautiful sandy beach near Townsville but were informed that at this season, the water was full of highly poisonous jellyfish that would paralyze any bather who attempted to swim there.

We then went to a resort area on the boundary between the provinces of Queensland and New South Wales, which supports a fine subtropical rainforest. As on other visits to such forests, I was greatly frustrated by the fact that flowers and fruits of its trees are borne so high above the ground that one cannot collect them without the aid of someone who can climb the trees. Another annoyance was the enormous number of leeches that attached themselves to every uncovered bit of my skin, so that a return to our hotel room had to be followed by an hour of pulling them off and staunching the blood they were sucking from me. Another nuisance was the presence of forest trees related to nettles, the foliage of which stung like fire whenever I brushed against it. I must admit that as a field botanist, I much prefer high and dry ecosystems to those of moist tropical climates. Nevertheless, visits with Australian botanists to open or semi-open areas in both Queensland and New South Wales in the Blue Mountains above Sydney enabled me to become familiar with *Tmesipteris*, one of the most primitive vascular plants in the Psilotaceae. In Sydney's Taronga Zoo, we saw the famous egg-laying mammal, the duck-billed platypus *Ornithorhynchus paradoxus* and, in a small forest area on the outskirts of the city, the Australian koala bear. The egg-laying mammal echidna[8] was abundant in both the Canberra and Sydney areas as well as in the Snowy Mountains that we visited with friends during the Christmas holidays. However, this animal that looks like a hedgehog has the same habits as its placental counterpart in Europe and defends itself by rolling up into a ball of spines whenever people or predators come near it, which it promptly did just when Barbara was attempting to take its picture. Barbara, however, was so determined to get a good photograph of it that I had to sit down on a rock for almost an hour and wait for the animal to unroll so that Barbara could get a picture that revealed its stubby snout and beady eyes.

The last trip of our visit to Australia was to the outlying island of Tasmania, which lies to the southeast of the continent. As in Australia proper, the forests of Tasmania consist chiefly of *Eucalyptus*. I had been told that Tasmania still supports trees of the largest species of this genus, *Eucalyptus regnans*, but when I got there I was informed that while the species is common, and I saw many moderate-sized trees belonging to it, the largest trees, which rival in height California's coast redwoods, are confined to a privately controlled commercial forest to which visitors are given access only by special permission. Nevertheless, the mountains that rise above the forest support a most interesting subalpine flora that contains many species endemic to the area. Our hosts were most cordial in showing us these areas, and I could only wish that I had time to study them more carefully.

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8. The duck-billed platypus *Ornithorhynchus paradoxus* Blumenbach is recognized as *Ornithorhynchus anatinus* Shaw. The Australian koala is *Phascolarctos cinereus* Goldfuss; the Australian echidna is likely the short-beaked spiny echidna *Tachyglossus aculeatus* Shaw. As egg-laying mammals or monotremes, the platypus and echidna belong to the unusual and primitive order Monotremata, distinct from marsupials in the order Diprotodontia to which the koala belongs. Taken from the American Society of Mammalogists, *Mammal Species of the World*, USNH, Botany, Smithsonian Institution. http://www.nmnh.si.edu/msw (2005). This website adapted from D. E. Wilson and D. M. Reeder, eds., *Mammal Species of the World* (Washington, D.C.: Smithsonian Institution Press, 1993). — VCH

From Hobart, Tasmania, we flew back to Sydney and across the Tasman Sea to New Zealand, where we were to be hosted on a series of visits beginning at Dunedin at the south end of the South Island and ending near the northernmost part of the North Island, the city of Auckland. From Dunedin, we visited two of the most spectacular sites that New Zealand has to offer. The first was a cave on the side of a lake that in its inner recesses supports a large population of glowworms, of which the eerie light reminded us of a fairyland palace.

The second site was Milford Sound, which is a drowned counterpart of our Yosemite Valley from which the precipitous craggy peaks rise to heights above the water that are comparable to the Half Dome of our Yosemite Valley. A big difference that in one way makes Milford Sound more spectacular than Yosemite is that whenever rainstorms come in, which is very frequently, the precipitous slopes are studded with waterfalls and veiled in mist. On the other side of the island, also near Dunedin, University of Otago botany professor Geoff Baylis, who had been my companion during much of our visit to Morocco in 1954 with the International Botanical Congress, showed us penguins waddling over the beach. We were most happy to see these birds in their natural habitat and could only wonder why they don't occur in the Northern Hemisphere. The most likely answer to this riddle is that the southern latitudes lack predatory carnivores such as bears and wolves that would make short shrift of any venturesome penguins attempting to establish themselves north of the tropics. From Dunedin, we went north to Christchurch, where I visited an experiment station for breeding grasses and other forage plants. We also went in the opposite direction to Arthur's Pass on the summit of the central mountain range, where we saw the New Zealand parrot or kea, a bird that seemed out of place near or above timberline. On this same drive, we visited a timberline station at which botanists were determining the factors that caused timberline to be where it is, using both native species and conifers introduced from the Northern Hemisphere. They found that the position of timberline is poorly correlated with the level of winter cold and freezing but, on the other hand, highly correlated with the mean temperature of the warmest summer months. Hence, although winters on the New Zealand mountains are no colder than they are in the North American Rocky Mountains or Sierra Nevada, summers at altitudes of 6,000 to 10,000 feet are much cooler than they are in our northern mountains, and this difference results in much lower timberlines in New Zealand than in North America at the same latitudes.

From Christchurch, we went north to Wellington and Palmerston North, the location of New Zealand's most important plant breeding station. We were most cordially received there by Margot Forde, who had received her Ph.D. degree with me at Davis. We then went on to Rotorua, which formerly supported a number of spectacular geysers. These are now capped and provide geothermal energy for many parts of the island. In Rotorua, the New Zealand Forest Service supports a tree breeding station from which seedlings had been provided for plantings of California's Monterey pine, which grows more luxuriantly in the island's climate than it does in California. The same is true to some extent near Canberra, Australia. In fact, while in Australia with a group of nature lovers, I noticed in a strictly native eucalyptus forest that was only a few miles away from a large planting of Monterey pine, a sapling pine that was obviously pushing its way to the sunlight through the eucalyptus cover. I called attention to this situation and remarked that "in a few years you will no longer have eucalyptus in this spot because they will be replaced by our Monterey pine.[9]"

They stared at me in horror and exclaimed, "Do you really think that those horrid pines will replace our beautiful eucalyptus?"

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9. Monterey pine, *Pinus radiata* D. Don. — VCH

I could not help remembering a similar conversation that took place in Berkeley shortly before I left for my trip. At that time, a severe winter had killed most of the eucalyptus trees in Tilden Regional Park, which adjoins Berkeley on the east. Our remarks had been, "Oh goody, now we can replace those awful eucalyptus trees with our own beautiful Monterey pines!" Apparently, the opinion on how beautiful trees are depends greatly upon where one lives and has been brought up.

From Rotorua, we returned to Auckland, where we renewed acquaintance with friends who had been with us at Davis and saw the splendid forest of kauri pine or *Agathis*. From there, we flew home via Tahiti for our fifth springtime in two years. The months of April and May in 1975 were occupied with renewing friendships in Davis and preparing for the next trip.

I had been able to secure an exchange fellowship for a six-week visit to the U.S.S.R., including attendance and a presentation at the XII International Botanical Congress in 1975. With the help of Armen Takhtajan, I had arranged for visits to the major institutions concerned with genetics and evolution. However, I soon found out that the arrangements could be canceled at will by the authorities. In my case, I had to maintain my policy of saying what I thought, which apparently did not make a good impression with higher authorities. When Barbara and I arrived in Moscow, we stayed at the hotel controlled by the U.S.S.R. National Academy and got the impression that everything we said to fellow guests and to each other was being carefully monitored and taken into account by the authorities.

After two weeks at the hotel, we had a splendid excursion to western Siberia and a suburb of Novosibirsk called Academy Town or Akadem Gorodok. This was situated in an open forest near the large reservoir that had been made by damming the Ob River. The laboratories were thoroughly modern, although I do not remember hearing about outstanding discoveries. My lecture on cytogenetics and evolution at the Congress was well received. We had plenty of time for walks in the woods, which were in full flower, and a most interesting excursion by motorboat on the lake. All in all, this was the most enjoyable part of our visit. When we returned to the hotel, I made a succession of visits, both to the government-run institutions and the Genetics Department of the University of Moscow. I met that department's leading plant cytogeneticist, Dr. Alexei Antonov, who was doing molecular research comparing different genera of the parsley family (Apiaceae). He has shown that the differences in fruit shape and structure that all taxonomists use to separate these genera are far less distinctive from the molecular point of view than one might expect from the data obtained by morphologists of the old school. For me, the high point of these visits was the Institute of Developmental Biology, where the principal investigations uncovered interesting facts about the transcription of RNA from DNA templates. It was there that I apparently pulled a faux pas about which I was informed when I got back to Davis and told my story to my colleague Mel Green. My last conversation before leaving this Institute was with its director, who asked me which of the laboratories I found to be most productive. When I named my choice, he seemed to look a bit unhappy. Later Mel Green explained that the departmental director to whom I spoke had a bad "odor" with the supervisor of the Institute because he did not follow faithfully the communist line.

Another institute that was directly in my line of interest was in charge of genetics and breeding of forage grasses and cereal grains. One of the projects that the institute had been emphasizing was the production of perennial wheat by hybridizing conventional, annual wheats to perennial quack grasses and then selecting for constancy and higher productivity in progeny. This kind of investigation had been started several years earlier when the charlatan T. D. Lysenko, a protegé of Stalin, was in full charge of genetics and breeding in the U.S.S.R. and still persisted after Lysenko had been deposed

about 1970. I could not detect evidence that the institute's researchers were anywhere near their goal, which my colleagues at Davis had called "impractical anyhow." This was because a perennial cereal must be kept in a dormant state during the winter, and the fields in which it grows cannot be made free of weeds before the next growing season.

While I was visiting institutes, Barbara was doing what she could to see more of Moscow. I joined her in two excursions. The first was to a monastery about 30 miles from the city that they showed us to demonstrate that religion was still being tolerated in the Soviet Union. The second we did on our own in the company of Irene Pipes, an American of Polish origin whose husband, Richard Pipes, was a historian specializing in Russian history. We took the subway to a railroad station, bought tickets with the help of Mrs. Pipes, and went to a station about 50 miles away, which was within walking distance of the former country home of a relative of Marinka Phaff, our close friend at Davis. This visit was most interesting. However, we discovered that we had traveled outside of the boundary around Moscow that was supposed to be the limit for foreign travelers. No doubt this breach of the rules was taken into account by the authorities.

In my schedule, I had left the visit to the most important of the institutes in Moscow to the end of my stay so that I could evaluate well what they were doing. This was the Institute of Molecular Biology. I had learned by that time that one always waits in the hotel to be picked up and taken to the Institute, and I did so on this final morning. After about two hours of waiting, I had a call put through to the secretary of the Academy that provided the transportation. They replied that we should be ready to leave for Tblisi, the capital of the state of Georgia, so that we could leave that afternoon.

Tblisi turned out to be most interesting, partly because a relative of our designated host there spoke excellent English and was particularly interested in things American. Translation of my talk on cytogenetics was handled easily, and I was given a fine visit to the Caucasus Mountains, which rise directly above the city. As in Morocco in 1954, I found that the subalpine vegetation of the area at the foot of Mount Kazbek was highly disturbed and overgrazed. I could not recognize any plants that I considered native but saw only common pasture grasses and weeds that are all over Europe. Georgia may contain productive institutes of botany and plant breeding as well as regions in which the flora is varied and interesting, but I didn't see them. From Tblisi, we flew directly to Leningrad (now St. Petersburg) and had about three days of visits before the beginning of the Congress. Both of us enjoyed greatly the Hermitage with its world-famous collection of paintings. The former palace of Tsar Peter the Great was also being kept up well, and we were taken through a succession of luxurious rooms and a smaller house near a lake where the Tsar spent much of his time.

The one scientific visit that I was most eager to make, to the cytogenetics laboratory of the Vavilov Institute for Genetics and Plant Breeding, turned out to be a frost. During the pre-Lysenko period from 1925 to the beginning of the war in 1941, it was the home of well-known cytogenetists such as Mikhail Navashin, G. A. Levitsky, and N. P. Avdulov, whose writings I had studied carefully both at Harvard and at Berkeley. However, when I was taken to the Institute, I was introduced to a man whose name I did not recognize and was asked to sit down with him. He spent the whole time that was scheduled for our visit talking about his program of bean breeding, which was of no interest at all to me. Apparently, the word had been spread that I was not to see research about which they were not sure that I would make complimentary remarks.

When the Congress began, Barbara and I were installed through the help of Professor Takhtajan at the principal hotel, recognizing that I was one of the vice presidents of the Congress. This gave us fine opportunities to talk with western European and American delegates and exchange opinions about experiences in the U.S.S.R. We were impressed with the great emphasis that the government placed on past experiences during

the war even though it had been over for 30 years. The billboard that advertised the moving pictures being shown contained titles replete with war experiences and lurid photographs of them. This theme was repeated in the hotel lobby, where two photographs were prominently displayed side by side. The one at the left was titled "The Nazis Said That They Would March Through the Streets of Moscow," and it showed the Nazis in full military uniform. The one at the right, titled "And They Did!," showed a long straggling line of men in rags of Nazi uniforms being herded by Russian soldiers through the principal streets of the capital.

I remember little about the proceedings of the Congress itself but, as always, it contained general reports of what had happened in our science during the previous six years. On the final evening, a splendid dinner was prepared, replete with ample dishes of caviar, plenty of vodka, and various other Russian savories. While I was talking with other delegates, a young man came up to me and asked, "Why didn't you visit our cytogenetics laboratory at the Vavilov Institute?"

I explained that a visit to the Institute had been scheduled before my arrival and that I had gone there at the appointed hour but had not been admitted to his laboratory.

"We can change all that," he said. "Can you visit us tomorrow morning?"

I could because my plane was not scheduled to leave until late afternoon, so he arranged to pick me up at 8:00 in the morning. However, when Barbara and I got back to our hotel room about midnight, we received a message from the desk saying that our bus would pick us up at 8:00 that morning to take us to the airport for our departure. Naturally I was not much amused. I am very satisfied that I saw the U.S.S.R. when I did and not really unhappy to have been a victim of its authority and power. Nevertheless, Barbara and I were particularly delighted when our plane arrived at the Helsinki airport and we had two glorious days to breathe the free air of Finland. From there, we went home and prepared for the fall semester at the university. I no longer had a formal teaching assignment but did take the opportunity to fill in when my colleagues wanted me to, principally in connection with graduate student seminars.

Chapter 30
Revisiting *Antennaria*

My next major assignment off-campus was at the University of North Carolina in the spring of 1976. I much enjoyed seeing the spring flora of the southeastern states and found interest in evolution to be high in both the University of North Carolina at Chapel Hill and Duke University at Durham.

The following year, 1977, initiated a new round of visits. First came Carleton College in Northfield, Minnesota. To get there, we had the dramatic experience, during the first week of January, of boarding a plane in Sacramento in an afternoon with a temperature 50 degrees above zero and landing at Minneapolis to a frigid 20 degrees below zero with wind chill that dropped it to 40 below. However, the cool reception from the climate was more than made up for by the warmth of hospitality given us by the Carleton faculty, especially its chairman of Biology, G. J. C. Hill, who almost immediately asked us to call him Gerry. My assignment was to give a course in general evolution similar to the one I had presented for many years at Berkeley and Davis. I found the students to be most receptive and intelligent and much enjoyed the informality of a small liberal arts college. Carleton is to the upper Midwest what Amherst and Williams are to New England and Reed College is to the Pacific Northwest.

During the first month of my stay, I enjoyed the skating rink on the campus and after that had a chance for botanical visits during the spring months. I was particularly pleased to see one of the most famous rarities of Minnesota, the Minnesota faunlily *Erythronium propullans*, which occurs only in a small reserve about 50 miles south of Northfield. To the north, we twice visited a reserve maintained by the University of Minnesota that contains a very fine *Sphagnum* bog similar to those I had known in Maine. In a nearby forest, we climbed a hill, which had a fire tower on top, so that we could look at the view. What we saw stretching to the limits of our vision in every direction was a vast expanse of forest and prairie without a single mountain or hill that cut through the skyline. When I realized that the nearest mountains or hills of consequence were 500 miles away to the north, 1,000 miles away to the southeast, and 1,500 miles away to the west, I thanked my stars that the university that had invited me to become a member of their faculty was the University of California rather than the University of Minnesota.

During the last month before leaving Carleton, I took the students on day trips and was able to show them examples of evolutionary diversity, which they appreciated. The result of all this was that at the end of my last class, a student came up to me bashfully and handed me an obvious present. It turned out to be a rewriting of the Twenty-Third Psalm in which the Lord was replaced by their professor of evolution. The punchline that I remember best was, "He leadeth us to green pastures, but usually he is a quarter-mile ahead of us."

When we got back from Carleton, spring was almost over. We went almost immediately to an apartment we had rented across the street from San Francisco State University, where I had a year's appointment as a visiting professor. During the fall semester, I taught my standard evolution course, followed in the 1978 spring semester by a course in heredity and evolution for nonmajors similar to the one I had been teaching at Davis. This student audience was at the same time less versed in botany or biology and more versed in general culture than any I had taught before.

I also learned that many students at San Francisco State University are just as good as the better students at Berkeley, but have to go to San Francisco State because they can easily commute to their homes and can find, in the big city, more jobs for which they earn more extra money than they could if they were living in Berkeley. One of the best students in my evolution course was even moonlighting as the assistant director of a ballet corps.

During the spring of 1978, I taught a small field course for students who had taken my lecture course in the fall. This gave me a chance to use their help in solving a problem that I had known about for a long time but for which I had not been able to obtain accurate data. Two of the best-known and obviously related species of oaks in coastal California are the coast live oak *Quercus agrifolia* and the interior live oak *Q. wislizenii*. I had seen populations near Santa Barbara in the south that seemed a mixture of the two species. The same species pair existed near Monterey where a small percentage of probable hybrids can be recognized. To the north of San Francisco near the University of California field station at Hopland, Mendocino County, these two live oaks appeared to be hybridizing to such an extent that the parental species were being swamped out. I used this example to illustrate situations in which the traditional species concept could be followed only by putting together two entities regarded as separate species by botanists and that occur sympatrically in most of California without intergrading or with only a small amount of such intergradation.

In the 1978 field course, we studied three areas. One of these was on the San Francisco Peninsula about 50 miles south of the city. The second was near Mount Tamalpais and a third was at Hopland. We used the methods developed by Edgar Anderson for estimating the degree of hybridization. We found that the frequency of hybrids was about 30 percent south of San Francisco and about 80 percent near Mount Tamalpais. At Hopland we verified my preliminary observation, every tree along the ranch road from Highway 101 to the station itself contained a mixture of characters belonging to *Quercus agrifolia* plus others more characteristic of *Q. wislizenii*.

After returning to Berkeley at the end of the summer of 1978, I went almost immediately to Columbus, Ohio, to become a visiting professor at Ohio State University and Barbara joined me after Christmas. The faculty of the Ohio State Botany Department greeted me cordially and my lectures went over well. While there, I remembered that while working on the genus *Antennaria* for my Ph.D. research, I had seen specimens in the Harvard Herbarium that suggested the presence of plants with male flowers from Ohio, whereas all of those from New England belonging to the species *A. parlinii* were strictly female in this dioecious species. In my work during 1929–30, I had learned to recognize two entities having large leaves. One of these had small flowering heads and populations containing male and female plants in about equal portions. The other kind had large heads and consisted only of females except that populations from the Washington area contained a few male plants. After I had spent a day with the specimens in the Ohio State Herbarium, I discovered that in Ohio as well as in neighboring Michigan, Illinois, and Missouri, all populations of the large-leaved group consisted of plants with large flowering heads and that in different localities male plants were present but in other localities they had not been collected.

I realized that my knowledge of *Antennaria* was sadly deficient because I had paid too much attention to the northeastern states and had neglected the Mississippi Valley. I immediately went to the chairman of the department and asked if the department could supply me with a small fund for investigating the problem during the forthcoming year. He replied that they didn't have any extra money but that if I could convince an incoming graduate student that the problem was worth his or her trouble as a project for a Ph.D., I would have help. I soon located Randall Bayer, who had just graduated from Cornell and was interested in chromosomes. I warned him that my own experience with counting

chromosomes and with raising seedlings from collected seeds had not been completely satisfactory, but he nevertheless was willing to take a chance.

We immediately collected seeds and brought in adult plants to raise in the greenhouse. His ability to count chromosomes from fixed and squashed root tips astounded me, as after about a month's work he had preparations so good that we could be sure of the number $2n = 84$ rather than 83, 85, or any other high number. This was true regardless of whether the plants were male or female. Also, the populations in Ohio contained within them so much variation with respect to the critical characters of plant pubescence and glandulosity that the species that had been recognized by both Fernald and me, *Antennaria fallax* and *A. parlinii*, had to be lumped into the species *A. parlinii* with the latter name having priority among botanists. Shortly afterward, Randy used accepted treatment methods for germinating seeds and obtained a large number of vigorous seedlings. His results showed me first, that the situation in the Midwest is quite different from that along the eastern seaboard and that second, Randy's quick grasp of critical methodologies would make it much easier for him to verify hypotheses via the cultivation and hybridization of plants than it was for me. We then showed his results to the faculty member who had become his major professor, Daniel Crawford. He gave Randy a lot of encouragement and said that the research they had planned to do together, obtaining enzyme patterns as a result of gel electrophoresis, would fit in well with the chromosome counting and hybridization experiments I had suggested.

In this way began the most rewarding association and friendship that I have had during my later years. Randy Bayer and I were very well adjusted to each other and could enjoy together the bits of humor as well as the more serious aspects of our research. In addition to his excellent flair for techniques, he also enjoyed mastering the nomenclatural aspect of systematics that I have had to follow but found boring. I followed his research for the rest of 1979. We took two long field trips together, one of them in 1980 and the other in 1984, after he had his Ph.D. degree and the year he was appointed to the University of Windsor in Ontario, Canada.

Randy and I were even able to persuade Arthur Cronquist that our arrangement of the eastern North American species of *Antennaria* was better than either his own or that of Fernald. During the spring of 1979, we discovered another interesting fact about the distribution of male plants in populations of *A. parlinii*. In regions where populations are large and close together as in central and southern Ohio, they usually contain male plants either in equal numbers or slightly higher proportions than those of female plants. In most of northern Ohio, Michigan, and central and northern Wisconsin, male plants are absent or rare and the plants produce seed via asexual means or apomixis, which I had already determined for most populations of *A. parlinii* from the eastern seaboard. Apparently, therefore, in this species the added variability provided by sexuality and obligate outcrossing is an advantage in regions most favorable for the species, but new areas can be successfully conquered only by apomicts that can be transported over long distances and will produce populations from a single colonizing individual via asexual means. After leaving Ohio and examining populations of other *Antennaria* species in the Sierra Nevada of California and the Cascade Mountains of Oregon, I reached similar conclusions about these different species.

Randy Bayer also developed new dimensions for judging relationships between species of *Antennaria*. He adopted the statistical method of multivariate analysis not available while I was doing my Ph.D. research. He also verified his results by collaborating with Daniel Crawford on allozymes. As a result, he obtained a new viewpoint about two of the species that I had studied previously. One of them was *A. virginica* that I had described in the 1930s and had believed to be the direct sexual ancestor of a more northern species belonging to the small-leaved group *A. neodioica*. Randy's evidence

showed that *A. neodioica*, although it probably contained a majority of its genes from *A. virginica*, also retained via hybridization, backcrossing or introgession, and polyploidy some genes derived from the large-leaved species, *A. plantaginifolia*. With respect to the large-leaved species, his evidence indicated that *A. parlinii* obtained its hexaploid chromosome number by combining the two genomes present in *A. plantaginifolia* with one of the western American species *A. racemosa*.

The trip in 1980 was the high-water mark in my relationship with Randy. In July, he picked me up at the airport in Rapid City, South Dakota. From there we drove together in his car through the Black Hills, the Big Horn Mountains of Wyoming, various mountain ranges in Montana, and on to Idaho, Washington, and British Columbia to join the evolutionists for the Second International Congress of Systematic and Evolutionary Biology at Vancouver. During all of this trip, neither of us saw anyone else we knew. We and the car were a unit in ourselves. Each new mountain range expanded our vista of the western species of *Antennaria* and provided the additional spice and adventure of exploring new territory. One event that for a while seemed too adventurous occurred in the Little Belt Mountains of Montana, which was the type locality for *A. umbrinella*, a key species of the small-leaved group. According to the map, our best course was to leave the car at the beginning of a narrow road that led to a mine and continue up the mountainside, where we hoped to find our plant. After a short upward climb, we found ourselves in a rock pile of hard quartzite, one of the most difficult types of terrain on any mountain. After almost exhausting ourselves on it, Randy said that he'd had enough and would start back toward the car. I was too eager to find the plant to turn back with him and said that I would meet him in front of the mine. About half an hour later, I too had had enough and had found an *Antennaria* that I thought might be the right one. I started down toward the mine hoping to see him there in front of the road that led back to the car. However, when I got there and had shouted several times, I did not see him nor did I get an answer to my calls. I therefore explored other paths leading outward from the mine until finally we met each other. After giving each other an affectionate hug and exchanging sighs of relief, we looked at the sky and realized that thunderheads had blown in so quickly and quietly that if we didn't hurry down to the roadhead where the car was, we would get soaked. In spite of our haste, it came upon us so soon that when we arrived at the car we were thoroughly soaked to the skin. Fortunately, the storm was brief enough so that we could light a fire and warm ourselves before supper. Still another thunderstorm struck us before we could get into our sleeping bags for the night. I hardly expected when I first started collaborating with Randy that there would come a time when Randy, who is just the age of one of my grandsons, would experience with me such an adventure.

Although Randy did well at the University of Windsor, he accepted an appointment at the University of Alberta, which is not only one of the larger and more prosperous Canadian universities but also is right in the middle of *Antennaria* country. Recently, he accepted the assignment of preparing an analysis of the genus for the forthcoming *Flora of North America*,[1] a comprehensive work encompassing multiple volumes.

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1. Now published in Flora of North America Editorial Commitee, eds., 1993+, Volume 19, *Flora of North America*, 12+ vols. (Oxford and New York: Oxford Univ. Press, 2006): 388–415.

Chapter 31
A Working Retirement

After returning from Ohio State, I spent about five to seven years in retirement but nevertheless was asked by the Davis Department of Genetics chairman Dick Snow to take over the graduate seminar on the history of genetics. This was a challenge for me. I could supplement the presentation with some of my own memories. Also, I had learned that in the preceding years this seminar had become an annoying prerequisite to the oral qualifying examination, chiefly because the students had not become prepared to make lively and interesting presentations of their topics. The practice that had been established and that I wanted to continue was for each student to select an important scientist in the field of genetics, to learn as much as possible about that person's activities and contributions, and to present this material to the class. The seminar was required as a preparation for teaching Beginning Genetics in an interesting way to future students. Consequently, I not only paid a great deal of thought to assigning topics to students but also spent a full hour in coaching them before each presentation. In this way, I developed a personal relationship with students interested in various aspects of genetics and with various backgrounds. Each year, the high point of the presentations was that of Watson and Crick and their discoveries of the DNA-RNA protein codes.

My next and last foreign trip was to Germany in 1987 for the XIV International Botanical Congress in Berlin, to Norway to make field studies of the two classic European species of *Antennaria*, and to Spain as visiting professor at the Universidad de León where the head of the genetics faculty, Marcelino Perez de la Vega, was my friend and associate as a previous visitor to Davis.

The Congress gave me a fine chance both to renew acquaintances with my European botanical friends and to get a glimpse of what younger workers in the field of evolutionary plant genetics were doing. The latter was particularly true because the secretariat did not ask me to present a general lecture as I had already presented several such lectures elsewhere in the past 20 years, but instead asked that I supervise and review the demonstrations of new discoveries on the part of younger botanists. Several of these demonstrations were truly original and promising. One that was particularly satisfying to me was by my friend Douglas Soltis from Washington State University at Pullman. He presented a series of examples of patterns of allozyme variation in natural polyploid species, both autopolyploid that did not have a background of hybridization at the diploid level and allopolyploid that were both polyploid and of hybrid origin. He then made a series of comparisons between what he had found by reanalyzing these polyploids using this modern technique that consists of extracting enzymes and determining their electrophoretic charges and recording similarities and differences between different populations and what I had predicted hypothetically on the basis of more traditional analysis and interpretations. In every case, he expressed agreement with my predictions. More rewarding than any honor that might have come from above was this reaffirmation from a bright young scientist of the research and theoretical hypotheses that I had developed during my lifetime.

After the Congress, I went to Oslo, Norway, to meet my friend Rolf Berg, who took me to two different locations in south-central Norway where the only two European

species of *Antennaria*, *A. dioica* and *A. alpina,* grow together. My objective was to learn whether the two species, when found in the same region, occupy different ecological niches. This is what I expected to find because I was reasonably sure that *A. dioica* had entered Norway from central and southern Europe, because it is not found at all in North America, while *A. alpina* had entered by long-distance dispersal from either Greenland or Iceland, because this species does not occur in Europe south of Norway and is equally absent from central and eastern Eurasia.

My expectations were partly realized, as in two altitudinal transects at the lower altitudes, *Antennaria dioica* was found while *A. alpina* was absent, and at the higher altitudes, *A. alpina* was the only species present. At intermediate altitudes, both species often occur side by side without any clear distinction in edaphic habitat. I decided to see if I could discover hidden differences by listing for each species the names of unrelated plant species that grew in contact with either *A. dioica* or *A. alpina.* In some localities, these lists of unrelated neighbors differed for *A. dioica* from those for unrelated neighbors of *A. alpina.* However, in a few sites, this difference was not observed. I had to conclude that both the climatic preferences and, in part, the edaphic preferences for the two species were different but that this difference could not always be recognized. In view of the fact that *A. dioica* is a sexual diploid that is not at all of hybrid origin, while *A. alpina* is an apomictic hexaploid that extends westward through Greenland to Alaska and is of hybrid origin from diploid taxa restricted to northwestern North America, this situation appeared to me most remarkable. During the first year after germination, their tiny seed develops into a rosette of leaves between one and two centimeters in diameter and obtains their entire mineral nourishment from the soil that underlies this small rosette. However, in later years, this rosette sends out a number of horizontal prostrate stems or stolons that root some distance from the original rosette. By the time one of these plants is ready to produce flowers and seeds, it may be one or more meters in diameter. Because each rosette may root in different soil regimes with the soil heterogeneous with respect to both water and nutrients, the ability of water and nutrients to pass via horizontal conduction along stolons or rhizomes greatly increases the ability of each plant to obtain a variety of both water and soil nutrients. Any inability of a seedling to obtain a full supply of all necessary elements would be affected by water and nutrient transport between rosettes. Naturally this hypothesis should be tested before being accepted indiscriminately. Nevertheless, it would explain the situation I found in Norway.

While in Norway, I was hosted not only by Professor Berg but also by his graduate students. One of them, Christian Brochmann, told me a most interesting story about his research on species of the genus *Draba.* He had compared allozymes in diploids and allopolyploids in two different species complexes. Other botanists and I doing research on polyploids always believed that allopolyploids that are of hybrid origin originate so rarely that repeated evolution of the same allopolyploid would be highly unlikely. On the other hand, Brochmann found, both in a white-flowered group and in a yellow-flowered group, such great differences in allozyme patterns between populations of what appeared to be the same allopolyploid occurring in regions remote from each other, that he could only conclude that they were of separate phylogenetic origin. Apparently, where polyploidy is involved, phylogenetic trees can be highly and unexpectedly complex.

Chapter 32
New York, The Rockefeller University, and the Nature of Molecules with Development

My experience at the Berlin Botanical Congress and my observations on *Antennaria* in Norway finished my research and theorizing on chromosome numbers and the nature of polyploidy. My second major interest, the phyletic tree of higher plants and the origin of the angiosperms, was essentially finished after the publication of my 1974 book, *Flowering Plants: Evolution Above the Species Level.* This left me with only one other major unsatisfied curiosity. This was the nature of processes concerned with the development of plants as a whole including the reproductive organs as well as leaves and stems. Beginning in 1988, I became aware of brilliant research being done in this field by Eliot Meyerowitz and his colleagues on a small annual of the mustard family, *Arabidopsis thaliana*, as well as similar work by Enrico Coen and his group on the snapdragon *Antirrhinum*.[1] These two research groups had identified genes that specify the stages of development of the plant fertile axis from the shift to reproductive activity, the formation of sepals, the formation of petals and stamens, and finally the formation of carpels and other ovule-bearing structures (the gynoecium).

I encountered a completely different aspect of development in two ways. In the first place, at a meeting of the Botanical Society of America more than 10 years ago, I heard about a completely biochemical way of altering development significantly. Dominick Basile showed that in several liverworts or Hepaticae, the phylogenetically primitive condition of the presence of branching and the arrangement of the leaflike phyllodes in threes was produced in the phenotype of a more advanced liverwort in which the secondary branching of the stems was normally absent and the phyllodes were paired rather than in threes. My discussion of this remarkable discovery led to periodic visits and discussion with Dominick, and I was hoping that we could become associated with each other during a longer period of time.

This opportunity occurred in 1990 in an entirely different way. About this time, I read an article by the Nobel Prize–winning molecular biologist G. M. Edelman in which he and his colleagues, in analyzing the development of complex structures in higher animals such as the feathers of a bird, refer to two kinds of molecules of a mixed character that in the same individual molecule combined the polypeptide chains of proteins with other hydrocarbon complexes most characteristic of carbohydrates in plant cell walls and various stored materials such as starch. Many of these molecules are known as glycoproteins, and this was the kind of molecule with which Basile was dealing. In plants, special glycoproteins exist in which the amino acid proline forms chains to which are attached hydroxyl residues. In his cultures of hepatics, Basile had recognized such molecules and had tested the effects of several different inhibitors of the attachment of hydroxyl residues to proline. The uniform effect of such inhibitors was applied to those species of hepatics that lack secondary branching with paired phyllodes.

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1. Particular publications as well as burgeoning modern research on plant development and evolution often utilizing *Antirrhinum* at the laboratory of Enrico Coen (John Innes Centre, United Kingdom) appear online through http://www.jic.bbsrc.ac.uk/staff/enrico-coen/Publications/Index.htm. — VCH

Basile had therefore shown that two particular morphological characters could be reversed by a significant biochemical change that affected particular glycoproteins. The development of a bird's feathers and that of the general architecture of a liverwort plant were generally similar in that, for the formation of both structures, glycoproteins were involved.

After thinking through all of these possibilities, I was increasingly perplexed. I therefore telephoned Dr. Edelman and asked for the best way out of my difficulty. He gave me a most encouraging reply. "Why don't you come to my institute in New York so that we can discuss these problems together? I can finance you for a visit of a few months duration."

He was as good as his word, so in January 1990, I was in the elegant quarters of his Institute for Neurobiology at The Rockefeller University in New York, while Barbara and I were given rooms in a nearby apartment house. She was ecstatic, and while I was busy working at the institute, she was busy with art exhibits, operas, and other musical events as well as shopping to the extent that we could afford. Edelman gave me a short interview upon my arrival and after that he was busy with his project of explaining mental behavior and consciousness as affected by Darwinian natural selection. Nevertheless, he financed two conferences on molecular biology and development of plants to which people were invited from many institutions throughout the United States. These conferences greatly broadened my knowledge although they did not lead directly to any publications. At the same time, I took advantage of the fact that Dominick Basile's laboratory was at Lehman College in the Bronx and he could drive down and pick me up so that we had many very fruitful discussions. One of the most delightful features of those days with Dominick was a series of lunches at an Italian restaurant run by a close friend of his. At that time, Basile had developed the hypothesis that many advanced specializations of plants originated from fundamental developmental changes. The more I thought about this theory in connection with the development of higher plants, such as angiosperms, the more I liked it.

For instance, the origin of oak trees, of which the ancestors had possessed staminate or male flowers and pistillate or female flowers that were much alike as they are in birches and alders, was through a combination of suppression and enhancement of developmental processes. On some branches, the function of producing gynoecia was suppressed while that of producing stamens was enhanced so that large quantities of wind-borne pollen might result. Conversely, on other branches, most of the staminate flower production was completely suppressed so that the developing gynoecia and protective leaflike scales were enhanced. Similarly, the evolution of cacti from their more mesic ancestors involved the suppression of leaves and the enhancement of the growth of stipular spines, plus the thickening or flattening of cacti stems.

Chapter 33
Final Activities

After this momentous visit to New York, I did relatively little in Davis except for promoting the cause of conservation by reviewing applications for financial help received by the California Native Plant Society from graduate students in botany. I also undertook one more trip to a national meeting and a second to Berkeley.

In January 1993, I received an invitation to attend a national symposium on molecular aspects of development in plants. As it was held in Taos, New Mexico, I asked Barbara if she would like to combine this trip with a general visit to New Orleans after the meeting. She decided that Taos was rather risky because she had a bad heart condition. I then decided to see if I could get an invitation to visit the Botany Department of Louisiana State University at Baton Rouge where the chairperson was a Ph.D. graduate from Davis, Shirley Tucker.

Shirley gave me a fine invitation, and Barbara and I decided to meet at the Dallas Airport immediately after the Taos Symposium and go together to Baton Rouge and New Orleans. She was most pleased to make reservations at places in New Orleans about which she had heard, and we were both looking forward to this final fling with great expectations. The Taos Symposium was highly instructive, and I was pleased to get the feeling that my research and thinking about plant development were on the right track.

During our stay in Baton Rouge, Barbara had a wonderful time visiting old plantation manors that were open to the public and chatting with caretakers and others who were interested in the cultural history of the South and Louisiana. I found that the students at Louisiana State University, many of whom had also been to Taos, were much interested in my seminar, and we had some really lively discussions about developmental and evolutionary botany.

On the last evening of the visit, we were invited to a reception at the home of Shirley Tucker and her husband, and a really joyful time was had by all of us. At 11:00 p.m. we went to the dormitory room that was provided for us on campus and fell asleep almost immediately. At 3:00 a.m., I woke up hearing a disturbance in the bed next to mine where Barbara had been sleeping. I looked over to see her spread across the bed in an unnatural position. I went across to find her completely limp and lifeless. I immediately telephoned the police, who came over with a coroner and pronounced her dead. When telephoned at her home, Shirley responded immediately and, with the greatest of sympathy, helped me settle affairs that were necessary before I left for home. A week later, we held a memorial service to which a great number of our friends came.

Fortunately, Barbara had realized the poor condition of her heart and felt that she might pass away at any time. She had therefore put all of our business affairs in the hands of one of her most intimate friends' daughter-in-law, Katie Pence. Unfortunately, Barbara's friend, Hazel Pence, passed away a few years after Barbara's death after a long struggle with cancer. Katie Pence then became my "guardian angel" and since that time has been diligently making life as pleasant as it can be without my dear Barbara. I am still doing projects from my home with the help of various caretakers, assistants, and friends, and I still enjoy working on theories and research. I still live in Davis. It has been and still is a good home to me.

The principal reflection that comes to me after recounting my life is that I am the only evolutionist whose career has included two of the major events to which evolutionists have been exposed during the 20th century. First, in 1926 when I was an undergraduate, I listened to a lecture by a leading professor of biology, G. H. Parker, who stated, in agreement with most biologists of that time, that Darwinian natural selection is only one of several theories to explain evolution, none of which was well founded. In my middle-age years from 1937 to 1950, I took part in the evolutionary synthesis of Darwinian natural selection that did firmly establish this process as one of the major processes of evolution. Finally, in my retirement years from 1973 on, I followed closely the advent and development of the molecular revolution in biology. I am convinced that in the future, information from DNA and other molecules must be considered before there will be further understanding of evolutionary processes.

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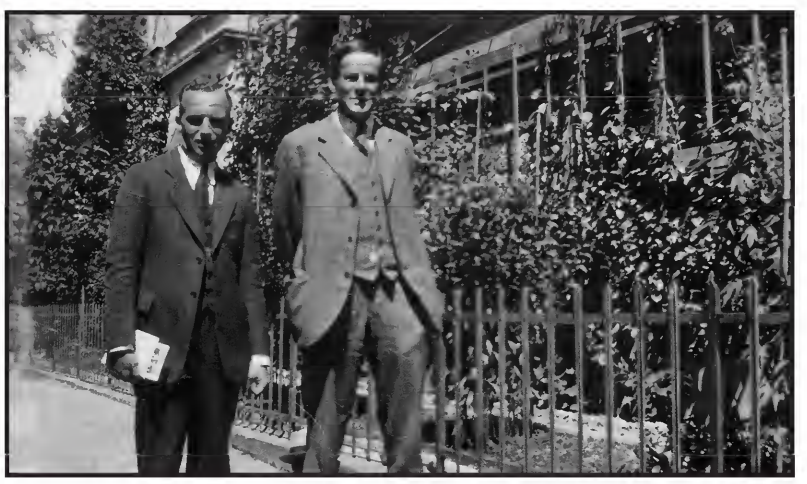
Images

1. George Ledyard Stebbins Sr. and Edith Stebbins with their children, George Ledyard Jr. (left), Marcia, and Henry, circa 1910.
Courtesy of Robert Stebbins

2. George L. Stebbins Sr., undated.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

3. Ledyard leads his horse, Querida, as his sister Marcia rides near their Santa Barbara home in the early 1920s.

4. Ledyard rows the family boat at Seal Harbor, Maine, in his college years in the late 1920s.



5. Ledyard and friend Rimo Bacigalupi wander the streets of Italy on a 1930 trip to Europe and the International Botanical Congress.

All images on this page from GLS personal collection, courtesy of Vassiliki Betty Smocovitis.

6. Ledyard (third from right in the second row from the top) thoroughly enjoyed his extracurricular activities as a second tenor in the Harvard Glee Club, shown here in 1928.
Courtesy of the Harvard University Archives, call # HUD 328.04

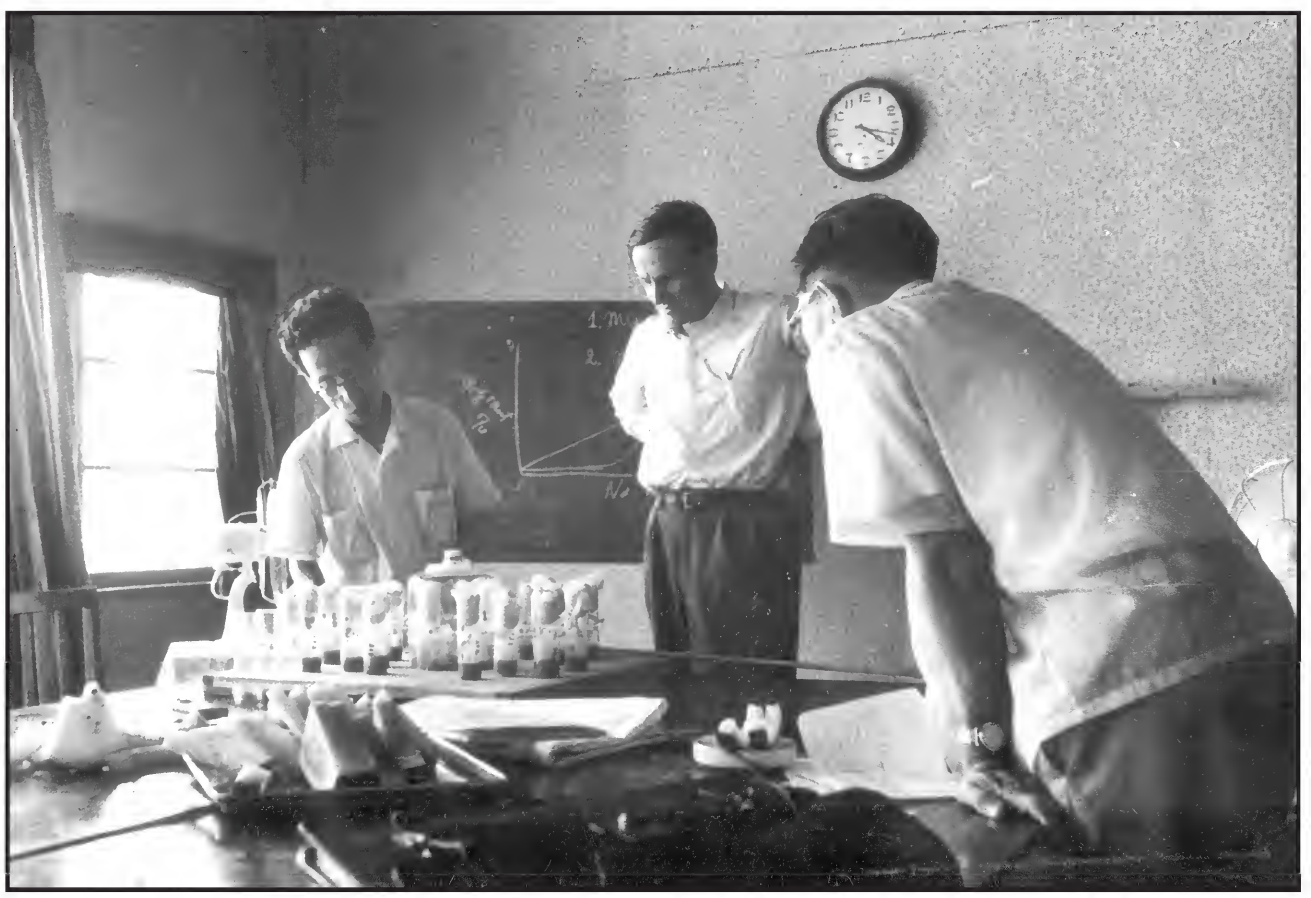
7 and 8. Ledyard and his first wife, Margaret (Peggy) Goldsborough Chamberlaine, in their 1931 wedding portraits.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

9. Ledyard's parents in 1935.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

10. The elder Stebbinses with Ledyard's children, George (left), Edy, and Bob in Santa Barbara, in November 1939.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

13. Ledyard talks genetics with Dr. Helen Spurway Haldane on a train ride near Tokyo during the 1956 International Genetics Symposium.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

14. Ledyard samples the local Japanese cuisine during the 1956 International Genetics Symposium.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis



15. Ledyard looks on as Dr. K. Sakai (left) demonstrates a remarkable population bottle at the National Institute of Genetics in Mishima, Japan, during Stebbins' visit to the 1956 International Genetics Symposium.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

16. Ledyard (standing) jokes at a gathering of colleagues at the University of California, Davis, in the 1970s. At the same table to his right is Harlan Lewis, and to his left is Theodosius Dobzhansky.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

17. Ledyard and his second wife, Barbara Monaghan Stebbins, in 1961 near Lund, Sweden.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

18. Stebbins shares refreshments and memories with Peter Raven in the spring of 1979 at Ohio State University, where Stebbins was serving a one-year visiting professorship. Raven was a guest speaker invited by Ohio State graduate students.
Courtesy of Vicki A. Funk

19. Ledyard poses in Cold Canyon Reserve, a California ecological study area named for him in a 1981 ceremony.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

20. Ledyard accepts the National Medal of Science from President Jimmy Carter in 1980.
GLS personal collection, courtesy of Vassiliki Betty Smocovitis

21. Ledyard lectures at Cornell University in 1987.
Courtesy of Vassiliki Betty Smocovitis. Print services by Ronald L. Stuckey, Ohio State University.

22. Barbara and Ledyard enjoy their retirement years at their home in Davis, California, in 1988.
Courtesy of Vassiliki Betty Smocovitis

23. Stebbins' childhood home in Seal Harbor still stands.
Courtesy of Vassiliki Betty Smocovitis

24. Ledyard with his biographer, Vassiliki Betty Smocovitis (from left), Kim Kleinman of Webster University, and Lee Kass of Cornell University at the XVI International Botanical Congress hosted in 1999 by the Missouri Botanical Garden in St. Louis.
Courtesy of Vassiliki Betty Smocovitis